A MONOGRAPH OF THE BALTIC AMBER BEES AND EVOLUTION OF THE APOIDEA (HYMENOPTERA)

MICHAEL S. ENGEL

Research Scientist, Division of Invertebrate Zoology,
Presently: Research Associate, Division of Invertebrate Zoology,
American Museum of Natural History;
Fellow, the Linnean Society of London;
Assistant Curator, Division of Entomology,
Natural History Museum and Biodiversity Research Center;
Assistant Professor, Department of Ecology and Evolutionary Biology,
1460 Jayhawk Boulevard, Snow Hall, University of Kansas,
Lawrence, Kansas 66045-7523

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 259, 192 pp., 123 figures, 7 color plates, 15 tables
Issued April 16, 2001
Price: $17.00 a copy

Copyright © American Museum of Natural History 2001 ISSN 0003-0090

Photomicrograph of the holotype (IMGP-K72) of *Glyptapis mirabilis* Cockerell.

CONTENTS

Abstract 5
Zusammenfassung 6
Introduction 7
  Historical Review 13
  Age and Origin of Amber 15
Materials and Methods 17
  Specimen Preparation and Study 18
  Format 18
General Morphology 19
  Prosoma 20
  Mesosoma 23
  Metasoma 32
Systematic Paleontology 33
  Superfamily Apoidea Latreille 34
  Division Apiformes 35
  Short-Tongued Versus Long-Tongued Bees 35
  Short-Tongued Bees 36
  Family Halictidae Thomson 36
    Subfamily Halictinae Thomson 36
      Tribe Halictini Thomson 37
        Genus *Electrolictus,* new genus 38
  Family Paleomelittidae, new family 41
        Genus *Paleomelitta,* new genus 42
  Family Melittidae Schenck 44
    Subfamily Macropidinae Robertson 46
      Tribe Eomacropidini, new tribe 46
        Genus *Eomacropis,* new genus 46
  Long-Tongued Bees 49
  Family Megachilidae Latreille 49
    Subfamily Lithurginae Newman 50
      Tribe Protolithurgini, new tribe 51
        Genus *Protolithurgus,* new genus 51
    Subfamily Megachilinae Latreille 53
      Tribe Osmiini Newman 54
        Genus *Glyptapis* Cockerell 56
        Genus *Ctenoplectrella* Cockerell 68
        Genus *Glaesosmia,* new genus 75
  Family Apidae Latreille 76
    Subfamily Xylocopinae Latreille 77
      Tribe Boreallodapini, new tribe 77
        Genus *Boreallodape,* new genus 78
    Subfamily Apinae Latreille 86
      Tribe Electrobombini, new tribe 88
        Genus *Electrobombus,* new genus 88
      Tribe Electrapini Engel 90
        Genus *Electrapis* Cockerell 92
        Genus *Protobombus* Cockerell 99
        Genus *Thaumastobombus,* new genus 109
      Tribe Melikertini, new tribe 112
        Genus *Succinapis,* new genus 115
        Genus *Melikertes* Engel 123

Genus *Melissites,* new genus 129
Genus *Roussyana* Manning 131
Tribe Meliponini Lepeletier de Saint Fargeau 133
Genus *Kelneriapis* Sakagami 134
Genus *Liotrigonopsis,* new genus 135
Apoidea Incertae Sedis 137
Genus and Species Indeterminate 137
Missing Taxa of Uncertain Identity 138
Cladistic Analyses 139
Lithurginae 139
Xylocopinae 140
Corbiculate Apinae 142
Discussion 150
Origin of Bees 150
The Eocene Bee Fauna 159
Epilogue 161
Acknowledgments 161
References 162
Appendix 1: Bees in Amber and Copal 175
Appendix 2: Tribal Classification and Geological Distribution of Bees 177
Appendix 3: Catalog of Family- and Genus-Group Names for Fossil Bees 180
Appendix 4: Full Titles of Journals Abbreviated in References 182
Index of Taxonomic Names 185
Color Plates 186–192

ABSTRACT

The bees found as Baltic amber inclusions are revised and the history of studies on these fossils is briefly reviewed. In total this subtropical Eocene fauna contains 36 species and 18 genera, all extinct. These are classified here into nine tribes, six subfamilies, and five families of which six tribes and one family are unknown in the modern fauna. The following taxa are described as new to science: **PALEOMELITTIDAE,** new family; **Boreallodapini, Electrobombini, Eomacropidini, Melikertini, Protolithurgini,** new tribes; **Ctenoplectrellina,** new subtribe; ***Boreallodape*, *Electrobombus*, *Electrolictus*, *Eomacropis*, *Glaesosmia*, *Liotrigonopsis*, *Melissites*, *Paleomelitta*, *Protolithurgus*, *Succinapis*, *Thaumastobombus*,** new genera; ***Boreallodape baltica*, *B. mollyae*, *B. striebichi*, *Ctenoplectrella cockerelli*, *C. grimaldii*, *Electrapis krishnorum*, *Electrobombus samlandensis*, *Electrolictus antiquus*, *Eomacropis glaesaria*, *Glaesosmia genalis*, *Glyptapis densopunctata*, *G. disareolata*, *Liotrigonopsis rozeni*, *Melikertes clypeatus*, *Melissites trigona*, *Paleomelitta nigripennis*, *Protobombus basilaris*, *Protolithurgus ditomeus*, *Succinapis goeleti*, *S. micheneri*, *S. proboscidea*, *Thaumastobombus andreniformis*,** new species (seven new family-, 11 new genus-, and 22 new species-group taxa). The genus *Electrapis* is found to be paraphyletic and the subgenera *Melikertes, Roussyana,* and *Protobombus* are given generic status outside of *Electrapis.* The subtribe Electrapina is elevated to tribal rank among the corbiculate Apinae and the subfamily Glyptapinae of Cockerell is reduced to subtribal rank within Osmiini. The genera *Chalcobombus* and *Sophrobombus* are newly synonymized with *Protobombus. Glyptapis reducta* Cockerell is synonymized with *G. fuscula* Cockerell, *Electrapis minuta* Kelner-Pillault with *Apis palmnickenensis* Roussy, *Ctenoplectrella splendens* Kelner-Pillault and *C. dentata* Salt both with *C. viridiceps* Cockerell, *Electrapis apoides* Manning and *Chalcobombus humilis* Cockerell both with *Protobombus indecisus* Cockerell, and *Electrapis bombusoides* Kelner-Pillault with *E. tornquisti* Cockerell (**new synonymies**). The following new combinations are proposed: *Electrapis martialis* (Cockerell), *Melikertes proavus* (Menge), *M. stilbonotus* (Engel), *Kelneriapis eocenica* (Kelner-Pillault), *Protobombus fatalis* (Cockerell), *P. hirsutus* (Cockerell), and *Electrapis martialis* (Cockerell) (**new combinations**). A lectotype is designated for *Electrapis minuta* Kelner-Pillault and neotypes designated for *Apis meliponoides* Buttel-Reepen, *A. palmnickenensis* Roussy, *Chalcobombus humilis* Cockerell, *C. hirsutus* Cockerell, *C. martialis* Cockerell, *Ctenoplectrella dentata* Salt, *C. viridiceps* Cockerell, *Electrapis tornquisti* Cockerell, *Glyptapis reticulata* Cockerell, *G. neglecta* Salt, *Protobombus indecisus* Cockerell, *P. tristellus* Cockerell, and *Sophrobombus fatalis* Cockerell. The subfamily Xylocopinae is recorded for the first time from amber, and the families Halictidae and Melittidae are confirmed as occurring in Baltic amber. The oldest fossils of the Halictidae, Megachilidae (Lithurginae and Megachilinae), Melittidae, and Xylocopinae are reported and described herein. Keys are presented for the identification of the Baltic amber bees. Three new recent taxa are also proposed: **Penapini, Redivivini,** and **Meliturgulini** (new tribes).

Cladistic analyses of the Lithurginae, Xylocopinae, and corbiculate Apinae are presented. Preliminary investigation of lithurgine relationships demonstrates that the fossil, *Protolithurgus,* is sister to extant genera of the subfamily and that *Lithurgus* s.s. is likely paraphyletic with respect to *Lithurgopsis* and *Microthurge.* Xylocopine relationships are generally in accord with those previously proposed: Xylocopini sister to all other tribes and Manueliini sister to the abruptly narrowed mandible tribes (i.e., Ceratinini, Allodapini, and Boreallodapini). Boreallodapini, despite some apparently apomorphic similarities with Ceratinini, is supported as sister to Allodapini. The paleontological evidence for corbiculate bee phylogeny reinforces traditional concepts over relationships of these tribes and contradicts recent molecular studies. Two extinct corbiculate tribes are based on specimens that exhibit worker morphologies indicative of advanced eusocial behavior and are related to the living, advanced eusocial tribes Apini and Meliponini, supporting a hypothesis of a single origin for this behavioral characteristic.

The composition of the Eocene bee fauna of Europe is discussed. The fauna is predominantly composed of long-tongued bees, but some short-tongued bees are represented in the families Halictidae, Paleomelittidae, and Melittidae. Bees in Baltic amber are generally allied with groups currently inhabiting sub-Saharan Africa and southeast Asia, a biogeographic pattern common to many Baltic amber groups.

The phylogeny and origin of bees are discussed. The bees are a derived, monophyletic

group of the spheciform wasps and presumably arose sometime in the earliest mid-Cretaceous after the origin of angiosperms. Reports of bees from Jurassic strata or earlier are all refuted. All available evidence supports the idea that bees originated shortly after flowering plants and diversified into higher lineages contemporaneously with the radiations of angiosperms. Major bee lineages (i.e., families) were thus presumably established by the Late Cretaceous.

A catalog of bees presently known in amber and copal is appended as is a catalog of family- and genus-group names for fossil bees (both amber inclusions and compression fossils). A preliminary outline of the tribal classification of Recent and fossil bees with their geological distribution is presented (with three new family-group taxa for living bees).

ZUSAMMENFASSUNG

Die als Inklusen des Baltischen Bernsteins nachgewiesenen Bienen werden revidiert und ihre Erforschungsgeschichte kurz dargestellt. Insgesamt umfasst diese subtropische Fauna des Eozäns 36 Arten und 18 Gattungen, die alle ausgestorben sind. Diese werden in neun Tribus, sechs Unterfamilien, und fünf Familien klassifiziert, von denen sechs Tribus und eine Familie in der heutigen Fauna unbekannt sind. Die folgenden Taxa sind neu für die Wissenschaft: **PALEOMELITTIDAE,** fam. nov.; **Boreallodapini, Electrobombini, Eomacropidini, Melikertini, Protolithurgini,** tribus nov.; **Ctenoplectrellina,** subtribus nov.; ***Boreallodape*, *Electrobombus*, *Electrolictus*, *Eomacropis*, *Glaesosmia*, *Liotrigonopsis*, *Melissites*, *Paleomelitta*, *Protolithurgus*, *Succinapis*, *Thaumastobombus***, gen. nov.; ***Boreallodape baltica*, *B. mollyae*, *B. striebichi*, *Ctenoplectrella cockerelli*, *C. grimaldii*, *Electrapis krishnorum*, *Electrobombus samlandensis*, *Electrolictus antiquus*, *Eomacropis glaesaria*, *Glaesosmia genalis*, *Glyptapis densopunctata*, *G. disareolata*, *Liotrigonopsis rozeni*, *Melikertes clypeatus*, *Melissites trigona*, *Paleomelitta nigripennis*, *Protobombus basilaris*, *Protolithurgus ditomeus*, *Succinapis goeleti*, *S. micheneri*, *S. proboscidea*, *Thaumastobombus andreniformis***, spec. nov. (sieben neue Familien-, 11 neue Gattungs-, und 22 neue Artengruppentaxa). Die Gattung *Electrapis* ist paraphyletisch, und die Untergattungen *Melikertes*, *Roussyana*, und *Protobombus* werden unabhängig von *Electrapis* als Gattungen akzeptiert. Die Untertribus Electrapina erhält den Rang einer Tribus innerhalb der corbiculaten Apinae, und die Unterfamilie Glyptapinae von Cockerell wird als Untertribus innerhalb der Osmiini interpretiert. Die Gattungen *Chalcobombus* und *Sophrobombus* werden neu mit *Protobombus* synonymisiert. Folgende Arten werden miteinander synonymisiert: *Glyptapis reducta* Cockerell mit *G. fuscula* Cockerell, *Electrapis minuta* Kelner-Pillault mit *Apis palmnickenensis* Roussy, *Ctenoplectrella splendens* Kelner-Pillault und *C. dentata* Salt beide mit *C. viridiceps* Cockerell, *Electrapis apoides* Manning und *Chalcobombus humilis* Cockerell beide mit *Protobombus indecisus* Cockerell, *Electrapis bombusoides* Kelner-Pillault mit *E. tornquisti* Cockerell (**neue Synonyme**). Die folgenden Kombinationen werden neu eingeführt: *Electrapis martialis* (Cockerell), *Melikertes proavus* (Menge), *M. stilbonotus* (Engel), *Kelneriapis eocenica* (Kelner-Pillault), *Protobombus fatalis* (Cockerell), *P. hirsutus* (Cockerell), und *Electrapis martialis* (Cockerell) (**neue Kombinationen**). Ein Lectotypus wird für *Electrapis minuta* Kelner-Pillault festgelegt. Für folgende Arten werden Neotypen designiert: *Apis meliponoides* Buttel-Reepen, *A. palmnickenensis* Roussy, *Chalcobombus humilis* Cockerell, *C. hirsutus* Cockerell, *C. martialis* Cockerell, *Ctenoplectrella dentata* Salt, *C. viridiceps* Cockerell, *Electrapis tornquisti* Cockerell, *Glyptapis reticulata* Cockerell, *G. neglecta* Salt, *Protobombus indecisus* Cockerell, *P. tristellus* Cockerell, und *Sophrobombus fatalis* Cockerell. Die Unterfamilie Xylocopinae wird erstmals in Bernstein nachgewiesen, und das Vorkommen der Familien Halictidae und Melittidae in Baltischem Bernstein wird bestätigt. Die ältesten Fossilien der Halictidae, Megachilidae (Lithurginae und Megachilinae), Melittidae, und Xylocopinae werden nachgewiesen und beschrieben. Bestimmungsschlüssel für die Bienen des Baltischen Bernsteins werden erstellt. Drei rezenten Taxa sind neu: **Penapini, Redivivini,** und **Meliturgulini** (tribus nov.).

Kladistische Analysen der Lithurginae, Xylocopinae, und der corbiculaten Apinae werden vorgestellt. Vorläufige Untersuchungen der verwandtschaftlichen Beziehungen der Lithurginae zeigen, dass die fossile *Protolithurgus* Schwestergruppe der rezenten Gattungen der Lithurginae ist. Außerdem ist *Lithurgus* s.s. wahrscheinlich paraphyletisch in Bezug auf *Lithurgopsis* und *Microthurge.* Die Verwandtschaftsbeziehungen der Xylocopinae stimmen grundsätzlich mit den bisher angenommenen überein: Die Xylocopini sind die Schwester-

gruppe aller übrigen Tribus, während die Manueliini die Schwestergruppe aller Tribus mit Arten mit abrupt verschmälerten Mandibeln ist (z.B. Ceratinini, Allodapini, und Boreallodapini). Boreallodapini wird als Schwestergruppe der Allodapini begründet, abgesehen von einigen anscheinend apomorphen Ähnlichkeiten mit den Ceratinini. Die paläontologischen Indizien stützen traditionelle Konzepte der phylogenetischen Beziehungen der corbiculaten Bienen und widersprechen neueren molekularen Untersuchungen. Die Arbeiter zweier fossiler, corbiculater Tribus zeigen morphologische Merkmale, die auf stark abgeleitetes eusoziales Verhalten hindeuten: Diese Tribus sind offenbar mit den rezenten, hoch-eusozialen Tribus Apini und Meliponini verwandt, was die Hypothese der einmaligen Entstehung dieses Verhaltensmerkmals unterstützt.

Die Zusammensetzung der eozänen Bienenfauna wird diskutiert. Sie besteht vorwiegend aus langzüngigen Bienenarten, auch wenn einige kurzzüngige Arten der Familien Halictidae, Paleomelittidae, und Melittidae ebenfalls vertreten sind. Im Allgemeinen sind die Bienen des Baltischen Bernsteins mit rezenten Bienen des Afrikas südlich der Sahara und Südostasiens verwandt; ein bei Organismen des Baltischen Bernsteins häufiges biogeographisches Muster.

Die Phylogenie und der Ursprung der Bienen werden diskutiert. Die Bienen sind eine abgeleitete, monophyletische Gruppe der spheciformen Wespen und entstanden irgendwann in der frühesten Mittelkreide nach der Entstehung der Angiospermen. Nachweise von Bienen aus dem Jura oder noch früher werden widerlegt. Alle verfügbaren Indizien stützen die Annahme, dass die Bienen kurz nach den Blütenpflanzen entstanden und in ihre grundsätzliche Diversifikation parallel zur Angiospermenradiation erfolgte. Die großen Linien der Bienen (z.B. Familien) waren daher in der späten Kreide bereits vorhanden.

Ein Katalog der in Bernstein und Kopal nachgewiesenen Bienen und ein Katalog der Familien- und Gattungsgruppennamen fossiler Bienen (sowohl aus Bernstein wie aus Sedimenten) wird vorgestellt. Eine vorläufige Idee einer Klassifikation der rezenten wie fossilen Bienen auf Tribus-Niveau mit ihrer geologischen Geschichte wird entwickelt (mit drei neuen Familiengruppennamen für rezente Bienen).

"*Et latet, et lucet Phaëtontide condita gutta,*
Ut videatur apis nectare clausa suo;
Dignum tantorum pretium tulit illa laborum,
Credible est ipsam sic voluisse mori."[1]

—M. V. Martialis, *Epigrammata,*
ca. 89 *anno domini*

Monographia Apum Succini Baltici

INTRODUCTION

Bees occupy a unique role in the world of arthropods. They are entwined into most aspects of human culture and mythology, not to mention our agriculture, economy, and general ecology. Mention of their name instantly recalls a suite of images and senses tying together warm days, sunny skies, soft breezes, and fields of fragrant and colorful flowers teeming with the gentle murmur of benevolent pollen harvesters at their labors. Bees have instilled within us ideal notions of industriousness, loyalty, obedience, and sacrifice not through denigration but through almost holy reverence to a greater good. Even the famous parable from the Bible (*Proverbs 6*) teaching us to "go to the ant" originally included reference to the labors of bees[2]. Such emotions and concepts connected to bees flow through our common natural heritage; even the great "Mother Goddess" uncovered at the root of most Western religions was symbolized by a bee.

More significant, perhaps, than their pervasiveness in human society is that bees serve as the most significant pollinators of flowering plants, helping to sustain and underpin major ecological systems worldwide

[1] Translation: "*Now dim, now bright, trapped in its amber tear, / A bee seems sealed in its own nectar clear; / For a life of endless toil, most fitting pay /—Surely a bee would wish to die this way!*" // Martial's *Phaëthontis* or "amber tear" is a reference to the myth of Phaeton, who died when he tried to drive the chariot of the sun across the sky. Phaeton's sisters wept and their tears turned to amber. Translation courtesy V. Krishna.

[2] "Go to the bee, and learn how diligent she is, and what a noble work she produces, whose labors kings and private men use for their use, she is desired and honored by all, and though weak in strength she values wisdom and prevails." *Proverbs,* Chapter 6, Septuagint version (i.e., the oldest Greek version and perhaps the oldest extant version) of the *Holy Bible* (see also Engel, 2000a: 2).

(e.g., Moldenke, 1976; Arroyo et al., 1982; Bawa et al., 1985; Bawa, 1990; Petanidou and Vokou, 1990; Buchmann and Nabhan, 1996; Proctor et al., 1996). The bees are also arguably one of the more diverse groups of pollinators, with a standing diversity of ca. 20,000 species. A phylogenetic study of the fossil record is crucial to understanding how this modern diversity came to be, as well as for identifying the periods of diversification and extinction, reconstructing historical zoögeography, and uncovering the sequence and origin of synapomorphies (e.g., Patterson, 1981; Grande, 1985; Eldredge and Novacek, 1985; Donoghue et al., 1989; Novacek and Wheeler, 1992; Grimaldi, 1992). The study of fossil bees, or *paleomelittology*[3], is still in its infancy and a complete synthesis of fossil and living taxa has yet to be achieved. The present work is one of a series of attempts to unite paleomelittology with the systematics of living bees into a meaningful whole. Fossils of bees are rare compared to some other insect groups; the few known specimens are typically discovered in isolation, and scattered in sites around the world. Three deposits, however, have produced sizeable bee paleofaunas.

Florissant, Colorado: Fossils from Florissant, Colorado, are compressions with virtually no relief, and were formed in fine volcanic ash over several millions of years of repeated eruptions. Preservation at Florissant can be quite fine, but those bees discovered to date typically preserve only the wing venation or some structures of the legs, so meaningful comparisons with other deposits or living taxa are not possible. Bees have been described from the families Halictidae, Andrenidae, Melittidae, Megachilidae, and Apidae (Cockerell, 1906, 1908a, 1908b, 1908c, 1909d, 1909e, 1911a, 1911b, 1913a, 1913b, 1914, 1917, 1923, 1925), although those of the Melittidae, Andrenidae, and some Apidae are dubiously assigned to family. These deposits have been dated at approximately 34.1 Ma (Epis and Chapin, 1974), placing them near the Eocene-Oligocene boundary, and are conservatively treated as early Oligocene herein. Work on the bees of these deposits is ongoing.

Dominican Amber: Bees in Dominican amber can be quite common; worker specimens of *Proplebeia dominicana* (Wille and Chandler) number into the thousands and can be frequently purchased in gem and mineral shops at no great expense. All other bee groups from these deposits are known on the basis of but a few individuals, often only one. Through a series of recent papers this fauna has been essentially revised. Table 1 summarizes the Miocene bee fauna of Hispaniola as it is presently understood. This paleofauna is quite modern in character. Most species are representative of extant genera, although several are today locally extinct from the West Indies (e.g., *Heterosarus, Neocorynura, Chilicola,* Meliponini) or from Hispaniola (e.g., *Euglossa, Eufriesea*). Those few Dominican amber genera that are extinct are remarkably similar to living forms. All groups are easily placed in living subtribes, tribes, and other higher categories.

The age of the Dominican amber mines has been of some controversy. Lambert et al. (1985) suggested a range of ages from Eocene to Miocene based on NMR analyses. Grimaldi (1995), however, argued that Dominican amber had to be younger than the Eocene and Oligocene dates, while Iturralde-Vinent and MacPhee (1996, 1999) later provided a strong stratigraphic basis for an early Miocene age. This geological evidence is also consistent with the inclusions in Dominican amber that are modern not only in general appearance but also in cladistic position (e.g., bees discussed briefly above; for flies see Grimaldi, 1995).

Baltic Amber: The middle Eocene amber of northern Europe was previously believed to contain merely a handful of specimens of rather rare and enigmatic bee species (e.g., Cockerell, 1908b, 1909b, 1909c; Zeuner and Manning, 1976). Although the few bees were recognized to be of phylogenetic import, the general paucity of material and the loss of several type specimens deterred meaningful work on the deposit. Through

[3] The word *paleomelittology*, admittedly of my own creation, is introduced here for the first time. It is derived from the Greek words παλαιοζ (*palaios,* meaning "ancient"), μελιττα (*melitta,* meaning "bee"), and λογοζ (*logos,* suffix denoting "knowledge of"). It can be defined as: (noun) the science of fossil bees; a branch of knowledge that deals with bees of past geological periods.

TABLE 1
Bee Fauna of Miocene Dominican Amber
(Updated from Engel, 1999d)

Taxa	References
FAMILY COLLETIDAE LEPELETIER DE SAINT FARGEAU	
Subfamily Xeromelissinae[a] Cockerell	
Genus *Chilicola* Spinola	
Chilicola electrodominica Engel	Engel, 1999f
Chilicola gracilis Michener and Poinar	Michener and Poinar, 1996
FAMILY HALICTIDAE THOMSON	
Subfamily Halictinae Thomson	
Tribe Augochlorini Beebe	
Genus *Augochlora* Smith	
Augochlora leptoloba Engel	Engel, 2000a
Genus *Neocorynura* Schrottky	
Neocorynura electra Engel	Engel, 1995
†Genus *Oligochlora* Engel	
Oligochlora eickworti Engel	Engel, 1996
Oligochlora grimaldii Engel	Engel, 1997
Oligochlora marquettorum Engel and Rightmyer	Engel and Rightmyer, 2000
Oligochlora micheneri Engel	Engel, 1996
Oligochlora rozeni Engel	Engel, 2000a
Tribe Caenohalictini Michener	
†Genus *Eickwortapis* Michener and Poinar	
Eickwortapis dominicana Michener and Poinar	Michener and Poinar, 1996
FAMILY ANDRENIDAE LATREILLE	
Subfamily Panurginae Leach	
Tribe Protandrenini Robertson	
Genus *Heterosarus* Robertson	
Heterosarus eickworti Rozen	Rozen, 1996
FAMILY MEGACHILIDAE LATREILLE	
Subfamily Megachilinae Latreille	
Tribe Megachilini Latreille	
Genus *Megachile* Latreille	
Megachile glaesaria Engel	Engel, 1999d
FAMILY APIDAE LATREILLE	
Subfamily Apinae Latreille	
Tribe Euglossini Latreille	
Genus *Eufriesea* Cockerell	
Eufriesea melissiflora (Poinar)	Poinar, 1998; Engel, 1999b
Genus *Euglossa* Latreille	
Euglossa moronei Engel	Engel, 1999b
Tribe Meliponini Lepeletier de Saint Fargeau	
†Genus *Proplebeia* Michener	
Proplebeia dominicana (Wille and Chandler)	Wille and Chandler, 1964; Michener, 1982
Proplebeia tantilla Camargo, Grimaldi, and Pedro	Camargo et al., 2000
Proplebeia vetusta Camargo, Grimaldi, and Pedro	Camargo et al., 2000

†Extinct genus. All Dominican amber species are extinct while most genera and all suprageneric groups are extant.

[a]The recognition of tribes in Xeromelissinae has recently been abandoned (Michener and Rozen, 1999), a decision which I have chosen to follow here.

diligent efforts over the past three years I have managed to increase the number of known specimens by nearly sevenfold and, as will be shown in the following pages of this monograph, the Baltic amber bee fauna is in actuality the most diverse extinct bee fauna known (summarized in table 2). Although I have increased the number of known individuals and species significantly, bees are still quite rare in Baltic amber, with only one specimen appearing among approximately every 5000 inclusions. Naturally, as work continues the number of specimens will grow steadily. I will be interested in examining new material as it becomes available for the production of supplements to this work. Since this monograph concerns itself expressly with the Baltic fauna, a discussion of the age of this amber is presented below (refer to Age and Origin of Amber).

Various other Cenozoic sites have produced bees (e.g., Late Cretaceous amber from New Jersey, Oligocene-Miocene amber of Mexico, Miocene compression from Japan, sundry Eocene through Miocene compression fossils in Europe and North America), and although work is continuing on these and other deposits (e.g., Engel, 1998c, 2000b, unpubl. data), none have at present revealed the number of individuals or diversity of bees exhibited by the above three locales. Moreover, most of these are compression fossils. If we seek to explore the implications of fossil taxa on our knowledge of bee evolution in general, then direct comparisons are required between often tiny or obscure morphological traits; such features are rarely preserved in even the finest of compression fossils. Amber, however, is unrivaled in the paleontological realm for its ability to preserve fine details (including internal tissues; e.g., Grimaldi et al., 1994) and so from at least those fossils of the Dominican Republic and the Baltic region we can begin to seek the necessary character information for comparison and eventual cladistic study. A further limitation arises, however; only one of the two major amber sites (i.e., Baltic amber; not surprisingly the older of the two deposits) has revealed taxa that are not essentially modern. As briefly mentioned above, the bees of the lower Miocene found as inclusions from the Dominican Republic

TABLE 2
Hierarchical Supraspecific Classification of Baltic Amber Bees
(Number of named species in each genus-group indicated)

FAMILY HALICTIDAE THOMSON	
Subfamily Halictinae Thomson	
Tribe Halictini Thomson	
†Genus *Electrolictus* Engel	1
†FAMILY PALEOMELITTIDAE ENGEL	
†Genus *Paleomelitta* Engel	1
FAMILY MELITTIDAE SCHENCK	
Subfamily Macropidinae Robertson	
†Tribe Eomacropidini Engel	
†Genus *Eomacropis* Engel	1
FAMILY MEGACHILIDAE LATREILLE	
Subfamily Lithurginae Newman	
†Tribe Protolithurgini Engel	
†Genus *Protolithurgus* Engel	1
Subfamily Megachilinae Latreille	
Tribe Osmiini Newman	
†Genus *Ctenoplectrella* Cockerell	3[a]
†Genus *Glaesosmia* Engel	1
†Genus *Glyptapis* Cockerell	4
FAMILY APIDAE LATREILLE	
Subfamily Xylocopinae Latreille	
†Tribe Boreallodapini Engel	
†Genus *Boreallodape* Engel	3
Subfamily Apinae Latreille	
†Tribe Electrobombini Engel	
†Genus *Electrobombus* Engel	1
†Tribe Electrapini Engel	
†Genus *Electrapis* Cockerell	4[b]
†Genus *Protobombus* Cockerell	5
†Genus *Thaumastobombus* Engel	1[c]
†Tribe Melikertini Engel	
†Genus *Melikertes* Engel	3
†Genus *Melissites* Engel	1
†Genus *Roussyana* Manning	1
†Genus *Succinapis* Engel	3
Tribe Meliponini Lepeletier de Saint Fargeau	
†Genus *Kelneriapis* Sakagami	1
†Genus *Liotrigonopsis* Engel	1

† Extinct.

[a] There is a single specimen of what may be a new *Ctenoplectrella* species or a new, closely allied genus. It was not included herein owing to exceedingly poor preservation and lack of additional material. Refer to genus *Ctenoplectrella*.

[b] There is at least one additional undescribed species (refer to genus *Electrapis*).

[c] Another specimen of this genus is perhaps representative of a second species. It is not described herein owing to too little information (refer to genus *Thaumastobombus*).

fall nicely into extant genera or into genera closely allied to living groups. Thus, although providing valuable information on local West Indian paleomelittology, extinctions, and patterns of historical biogeography, Dominican taxa contribute little to our knowledge of bee phylogeny. In fact, a general comparison (of all deposits) of bees from the Oligocene to the present day shows very little difference in the fauna at the generic or higher levels (refer to Discussion, below).

Early statements pertaining to Baltic amber bees were tantalizing: "With the general form of *Apis* [honey bees], it has venation nearer to that of *Bombus* [bumble bees]. . . " (Cockerell, 1909b: 8). Observations like these, combined with the much older age of Baltic amber, make a study of those taxa all the more enticing and critical. Now, with so many more Baltic specimens at hand, it is possible to confirm the observations of earlier authors, to add numerous newly discovered lineages to the list of known taxa, to carefully and systematically describe such peculiar groups, to explore the phylogenetic implications of these taxa, and to make more general observations and hypotheses on the origin, diversification, and evolution of the bees. As the following pages demonstrate, the Baltic amber bee fauna is the best documented paleofauna for bees, the most diverse (in both numbers of species, genera, and other higher categories), and the most critical for phylogenetically important taxa. The Baltic amber is the oldest deposit in the world with a bee fauna of any sizeable significance.

This work is, in essence, a faunal revision, the area under consideration being the Baltic region of 45 million years ago. As with any faunal revision there is concern over whether or not the author took a global view when delimiting groups and thereby avoided proposing synonyms for taxa well characterized outside of the limited geographic scope of the work. I hope to eliminate this potential criticism at the start by stating that, although dealing with a bee fauna that has long since vanished from the Earth, I took an exhaustive geographic and temporal perspective when analyzing these fossils. Not only were fossils studied from all existing deposits containing bees (of all ages, Cretaceous to Pleistocene!), but the living fauna was considered on a global scale. Moreover, many of the fossils have been included in cladistic studies with living groups so as to better define their affinities to known lineages and the validity of basing taxa on their peculiar character combinations. This has manifested itself most notably for the corbiculate Apinae. Numerous fossils of this clade occur in Baltic amber, and owing to the controversy concerning relationships among Recent corbiculates (e.g., Schultz et al., 1999), it has been particularly critical to document the morphology and cladistic implications of the extinct corbiculate taxa (Engel, 2000c). As a result of this body of work, the classification of Baltic amber bees has been radically altered (table 3).

A recent classification of the bees (Michener, 2000a) recognized seven extant families: Colletidae, Stenotritidae, Halictidae, Andrenidae, Melittidae, Megachilidae, and Apidae. The classification presented here also recognizes seven families in total but differs in two major groupings from that proposed by Michener (2000a). The family Stenotritidae is a clade of Colletidae and renders the latter paraphyletic; as mentioned elsewhere (e.g., Engel, 2000a: 5), I consider *Stenotritus* and *Ctenocolletes* to form a subfamily of Colletidae, although stenotritines should perhaps be further demoted to tribal rank within Colletinae (or perhaps more appropriately, the latter group should be broken into several subfamilies). Furthermore, I have recognized a new family from the fossil record (described below) that is intermediate in character between the basic short-tongued families and a clade consisting of Melittidae and the long-tongued bees. Lastly, with regard to the familial classification, I believe sufficient evidence exists for Melittidae monophyly so as to retain it as a single family, thereby avoiding the proliferation of "melittoid" families suggested by Alexander and Michener (1995: Melittidae s.s., Dasypodaidae[4], and Meganomiidae). Appendix 2 along with figures 122 and 123 summarize my suprageneric classification of bees as it

[4] The original spelling for this subfamily, Dasypodinae, has been emended in order to remove homonymy with the family-group name for armadillos (Mammalia: Xenarthra: Dasypodidae) (Alexander et al., 1998; ICZN, 1999a).

TABLE 3
Comparison of Present Classification with Earlier Usage

Present Classification	Most Common Earlier Usage
APIDAE: Apinae	
Electrobombini	
Electrobombus samlandensis Engel	New herein
Electrapini	
Electrapis krishnorum Engel	New herein
Electrapis martialis (Cockerell)	*Chalcobombus martialis*
Electrapis meliponoides (Buttel-Reepen)	*Electrapis meliponoides*
Electrapis tornquisti Cockerell	*Electrapis tornquisti*
Protobombus basilaris Engel	New herein
Protobombus fatalis (Cockerell)	*Sophrobombus fatalis*
Protobombus indecisus Cockerell	*Protobombus indecisus, Chalcobombus humilis*
Protobombus hirsutus (Cockerell)	*Chalcobombus hirsutus*
Protobombus tristellus Cockerell	*Protobombus tristellus*
Thaumastobombus andreniformis Engel	New herein
Melikertini	
Melikertes clypeatus Engel	New herein
Melikertes proavus (Menge)	*Electrapis proava*
Melikertes stilbonotus (Engel)	*Electrapis stilbonota*
Melissites trigona Engel	New herein
Roussyana palmnickenensis (Roussy)	*Electrapis palmnickenensis, Electrapis minuta*
Succinapis goeleti Engel	New herein
Succinapis micheneri Engel	New herein
Succinapis proboscidea Engel	New herein
Meliponini	
Liotrigonopsis rozeni Engel	New herein
Kelneriapis eocenica (Kelner-Pillault)	*Kelneriapis eocenica, Hypotrigona eocenica*
APIDAE: Xylocopinae	
Boreallodapini	
Boreallodape baltica Engel	New herein
Boreallodape mollyae Engel	New herein
Boreallodape striebichi Engel	New herein
MEGACHILIDAE: Lithurginae	
Protolithurgini	
Protolithurgus ditomeus Engel	New herein
MEGACHILIDAE: Megachilinae	
Osmiini	
Ctenoplectrella cockerelli Engel	New herein
Ctenoplectrella grimaldii Engel	New herein
Ctenoplectrella viridiceps Cockerell	*Ctenoplectrella viridiceps, C. dentata, C. splendens*
Glaesosmia genalis Engel	New herein
Glyptapis densopunctata Engel	New herein
Glyptapis disareolata Engel	New herein
Glyptapis fuscula Cockerell	*Glyptapis fuscula, G. reducta*
Glyptapis mirabilis Cockerell	*Glyptapis mirabilis*
MELITTIDAE: Macropidinae	
Eomacropidini	
Eomacropis glaesaria Engel	New herein
PALEOMELITTIDAE	
Paleomelitta nigripennis Engel	New herein
HALICTIDAE: Halictinae	
Halictini	
Electrolictus antiquus Engel	New herein

presently stands; more detailed studies and further refinements will be presented elsewhere.

Historical Review

Baltic amber has had a long association with humans, perhaps more so than any other amber deposit. The first Baltic amber bees were simply mentioned rather than described or studied in any detail. Authors of antiquity regularly referred to amber and insect inclusions and, owing to the already tight bond between bees and man by the Hellenic and Roman eras, it is little wonder that even fossil bees would appear in their literature (e.g., the poem at the opening of this monograph; the work of Ausonius).

Burmeister (1831, 1832) seems to have been the first researcher to comment on the presence of bees in Baltic amber after the standardization of binomial nomenclature by Linnaeus (1758). In his works he refers to a "*Trigona*" similar to South American species. None of his material has survived to the present day; however, individuals of the melikertine bees have a general habitus strongly reminiscent of *Trigona* species and it is possible Burmeister had one of these bees before him. Hope (1836) also mentioned bees in his private collection of Baltic amber insects as well as in the collections of his correspondents. Hope referred in his synopsis of amber insects to specimens of "*Andrena*", "*Apis*", and "*Trigona*" (the latter two perhaps included specimens of Electrapini and Melikertini, respectively, or were actually living taxa preserved in copal[5]).

Menge (1856) was the first to describe some of the forms he had before him as new species of extant genera, naming species of what he believed to be *Apis* and *Bombus.* In addition, Menge referred to individuals of *Anthophora, Dasypoda,* and *Osmia,* although he did not give them specific names. After a diligent search it appears that only one of his specimens has survived to the modern day, this being his *Apis proava* (treated below as *Melikertes proavus*). Owing to the misplacement of this species, even following the taxonomic conventions of his time, Menge's remaining species must be considered dubiously assigned as to genus. Motschulsky (1856), working at the same time, recorded a specimen of "*Andrena*" and proposed the genus and species *Bombusoides mengei*; the latter becoming the first new genus-group proposed for the fauna and the first recognition of an extinct supraspecific lineage from the Baltic amber. Brischke (1886) later identified what he considered to be *Andrena, Chalicodoma, Anthophora, Melipona,* and *Bombus* in Baltic amber, but none were given names. Like much of Menge's material, the specimens examined by Burmeister, Brischke, and Motschulsky have been presumably lost. All of these authors, except, of course, Motschulsky, placed the specimens before them into Recent genera and species groups. None of the identifications by these authors can be considered entirely accurate and should not be relied upon for determining the presence of a particular living bee genus in Baltic amber nor for placing a middle Eocene age on any of these same genera.

Buttel-Reepen (1906) was the first researcher of the last century to systematically study a Baltic amber bee as part of his larger monograph on the honey bees of the world. In his study, Buttel-Reepen described a Baltic amber fossil as *A. meliponoides* and considered it as intermediate between the honey bees (tribe Apini) and their sisters, the stingless bees (tribe Meliponini); hence his choice of a specific epithet. *Apis meliponoides,* despite Buttel-Reepen's contention, does not fit into this position (see below), although there are indeed Baltic amber fossils that appear intermediate in some characters between Apini and Meliponini and strengthen their sister-group relationship supported by numerous authors (e.g., Engel, 1998d; Noll, 1998; Schultz et al., 1999, and references therein).

Cockerell was the next individual to undertake a study of the Baltic amber bees and in far greater depth than Buttel-Reepen, who was primarily interested in *Apis.* In a series of papers published in 1908 and 1909, Cock-

[5] Examination of surviving material from Hope's collection in the University Museum, University of Oxford, has revealed only specimens of extant *Hypotrigona* and one *Heriades* in African copal (mistakenly identified as succinite). It is possible that all of Hope's original material was actually copal, although that material he reports on from his contemporaries' collections certainly included true Baltic amber. I am grateful to C. O'Toole for a loan of this interesting material.

erell described the majority of the Baltic amber bees known until the completion of the present study. Cockerell was intimately familiar with the world bee fauna and was the first to recognize the significance of the Baltic amber bees, attempting, in a very rudimentary way, to explore the implications of these taxa on apid evolution (e.g., Cockerell, 1908b) (fig. 120).

Subsequent to Cockerell only a few workers have attempted to study the Baltic amber bees, none in great detail. Only two small papers appeared between the work of Cockerell and a small outburst of activity in the 1970s. Salt (1931) proposed new species of *Glyptapis* and *Ctenoplectrella* as well as a species he believed to be an *Andrena* (see Apoidea Incertae Sedis, below), while Manning (1960) described a new species of what he believed to be *Electrapis* along with a new subgenus. Outside of these two works, systematic study of bee inclusions from the Baltic stagnated for about one-half of a century. It was not until the papers of Kelner-Pillault, late curator of Hymenoptera at the Museum National d'Histoire Naturelle, that scientific study of this fauna resumed, although for only a very short while. Kelner-Pillault engaged herself in five short studies of bees from these deposits. Although her work was adequate, she did not attempt to question previous studies nor to compare her material to prior descriptions, thereby forcing her specimens into new taxa within groups as defined by earlier authors. Curiously, Kelner-Pillault published erroneous information for the type depositories of species she described (e.g., Kelner-Pillault, 1970a, 1970b). In her papers she regularly refers her material to the Institut und Museum für Geologie und Paläontologie in Göttingen, when nearly all of her material is in the Institut für Paläontologie, Museum für Naturkunde, in Berlin. It cannot be that the specimens were simply sent to the wrong institution after publication, since each is accompanied by older labels that catalog them as belonging to Berlin (and these are often quoted by Kelner-Pillault in her papers). This unfortunate confusion is the reason it has been difficult for other workers to locate and study her material [e.g., Michener (1990) records that he was unable to locate *Trigona eocenica* in Göttingen as indicated in Kelner-Pillault's paper; the type was actually in Berlin]. All of this information has been corrected below.

The last major work on the Baltic amber fauna was as part of a larger attempt to monograph all fossil bees (Zeuner and Manning, 1976). This work was compiled from accumulated notes more than a decade after the deaths of the authors and as such unfortunately suffers from a number of errors. Most of their monograph does not present original information and often the sections for a given taxon are merely taken from the original descriptions. This is particularly true for the Baltic amber bees. In several instances it is all too apparent that neither had ever seen specimens of particular taxa (e.g., see sections on *Ctenoplectrella* and *Glyptapis,* below). Moreover, in their work some taxa have been incorrectly diagnosed owing to a failure to examine types (e.g., *A. henshawi*; see Engel, 1998c), and the authorship attributed to numerous groups is wrong. Researchers should be mindful of these difficulties and proceed with caution when attempting to use their monograph. Had both Zeuner and Manning lived longer, the study doubtless would have been a more accurate and beneficial work.

Since the 1970s almost nothing has appeared on the Baltic amber bee fauna. Of the minor references to Baltic amber bees in recent literature only two papers deserve mention. Both Gerlach (1989) and Engel (1998a) presented short notes on small collections of specimens. Gerlach (1989) reported three specimens misidentified as *Dasypoda, Megachile,* and *Apis* (identifications corrected herein as *Glyptapis, Ctenoplectrella*?, and *Electrapis,* respectively), while Engel (1998a) described a new species and subgenus in *Electrapis* and commented on the classification of the genus as it was understood at that time (that classification is radically altered herein). Although reference to the enigmatic nature of Baltic amber bees has often been made (e.g., Winston and Michener, 1977; Michener, 1990; Engel, 1998a), as well as the desperate need for a critical revision and reexamination of the fauna (e.g., Lutz, 1993), the field has remained essentially untouched.

The present work is an attempt to monograph this unique fauna of bees, to explore its implications for understanding higher-level affinities of apoid taxa, and to consider general evolutionary patterns of the bees inclusive of their early origins. This is the first comprehensive treatment of a fossil bee fauna and is part of a series of papers by the present author to monograph the fossil bees of the world, ultimately aimed at unifying paleomelittology with our neontological knowledge of bees. Future revisions of this monograph will undoubtedly be needed as new or more perfectly preserved specimens are discovered. For the present, however, I hope that this work will provide a foundation for paleoentomological studies of bees. A catalog and bibliography of the fossil bee species of the world (both amber inclusions and compression fossils) is currently in preparation (Engel, in prep.), while a catalog of family- and genus-group names for fossil bees is appended at the end of this work (appendix 3).

Age and Origin of Amber

Although pockets of Baltic amber can be found throughout northern Europe (e.g., Denmark, Sweden, Germany, Poland, and Lithuania, among other countries), the greatest concentration, and where most material originates, occurs on the Samland Peninsula (historically part of Prussia but today occupied by Russia). The city of Königsberg (today Kaliningrad), situated near the base of the Samland Peninsula, once held the most significant and largest collection of Baltic amber inclusions owing to the proximity of the richest deposits. The Albertus Universität in Königsberg was estimated to hold some 100,000 inclusions at one time. This material was actively studied for a number of years, particularly by the Königlichen Physikalisch-Ökonomischen Gesellschaft (Royal Physical Economy Society), which began publishing special works on Baltic amber in 1860 and continued until 1938. Significant works on insect inclusions were produced for ants (Wheeler, 1914), apterygotes (Olfers, 1907; Silvestri, 1912), and, of course, the studies by Cockerell (1909b, 1909c) on bees, among others. Tragically, Albertus Universität suffered, alongside millions of people and other cultural institutions, during the second World War, and the collection was mostly destroyed, although some surviving specimens were scattered for safekeeping. Today, the largest surviving portion from Königsberg's collection is located in the Institut und Museum für Geologie und Paläontologie in Göttingen, although it is still only a fraction of the original collection's size.

Baltic amber occurs in the *blau Erde* ("blue Earth"), which, as mentioned above, occurs throughout northern Europe approximately 45 m below the surface and runs ca. 5 m below sea level. Thus, exposed deposits can erode out and wash amber up on shores not only of the Baltic countries but as far away as the eastern coasts of England. The formation continues under the Baltic sea floor. Stratigraphic studies of the *blau Erde* indicate it to be middle Eocene in age (Kosmowska-Ceranowicz, 1987; Kosmowska-Ceranowicz and Müller, 1985). The stratigraphic dates correlate perfectly with recent K-Ar radiometric studies (Ritzkowski, 1997), all of which indicate that Baltic amber is 44.1 ± 1.1 Ma, placing it in the middle of the Lutetian stage of the Eocene Epoch. The Bitterfeld amber (or Saxonian amber) from Germany is actually contemporaneous with Baltic amber and similar in both chemical composition and inclusions of the fauna and flora (e.g., Schumann and Wendt, 1989; Röschmann and Mohrig, 1995). This Eocene amber occurs in Miocene strata and has therefore been considered to be much younger than true Baltic amber; however, it has been demonstrated that Bitterfeld amber has been redeposited at least twice during its geological history (Weitschat, 1997). Bitterfeld amber is, in essence, Baltic amber that has been eroded and redeposited in Miocene formations. A few of the inclusions studied herein are in Bitterfeld amber and are identical to taxa from true Baltic amber (see below).

Pieces of Baltic amber can be readily identified by a number of diagnostic features. The succinic acid content of most Baltic amber is relatively high (ca. 8%); this is the reason it is commonly referred to as succinite. Some more rare deposits, however, either lack suc-

cinic acid (e.g., glessite, gedanite), or possess it in only trace amounts (e.g., beckerite). The chemical composition of Baltic amber, however, is relatively uniform and diagnostic by comparison with all other amber deposits. Analysis using pyrolysis gas chromatography of Baltic amber produces a diagnostic set of peaks (Shedrinsky et al., 1991) and, similarly, infrared spectroscopy analysis produces a characteristic absorption spectrum with the unique "Baltic shoulder" between 1250–1175 cm^{-1} (Beck et al., 1964, 1965; Beck, 1986). Pyrolysis GC analysis of Bitterfeld amber is identical to that of true Baltic amber (Shedrinsky et al., 1991). Additionally, Baltic amber frequently includes numerous stellate trichomes (plant hairs), and inclusions are sometimes covered, either partially or entirely, in *Schimmel* (a whitish froth of microscopic bubbles resembling mold: e.g., pl. 7a).

Although it has been understood since antiquity that amber (from northern Europe in particular) is the petrified resin of ancient trees, the botanical origin of Baltic amber is still debated (although a final solution is perhaps on the horizon). Both Pliny the Elder (in his *Natural History*) and Tacitus (in his *Germania*), writing around the same time during the 1st century, record the ancients' understanding of the resinous origin of amber. Tacitus noted that, "The Germans gather amber but they have not investigated the natural cause or process. . . It is sap [Tacitus's term] from trees, which can be inferred from the fact that you can see creeping things and winged insects which were trapped when the substance gradually hardened", while Pliny further elaborated on the processes producing amber when he wrote "Amber is formed of resin seeping from the interior of pine trees. . . The exudation was hardened by cold or heat or by the sea. . . That amber originated as sap is proved by the visible presence of gnats, ants, and lizards trapped inside as it hardened". Most authors, like Pliny, have attributed these resins to a member of the pine family (Pinaceae) and to the extinct species *Pinites succinifer* Göppert (1836). Although arguments have been made for Araucariaceae (e.g., Langenheim, 1969; Poinar and Haverkamp, 1985), the pinaceous hypothesis retains significantly stronger support. Among the thousands of inclusions in Baltic amber are numerous cones and needles of pines (e.g., Weitschat and Wichard, 1998) as well as wood fragments with microstructural characters indicative of Pinaceae (Pielinska, 1997; Turkin, 1997). There are no araucariaceous inclusions in Baltic amber, and all studies of the botanical inclusions, particularly those of wood fragments, have not identified any features distinctive to Araucariaceae (*Agathis,* in particular). Enigmatically, most pines today do not produce succinic acid and Baltic amber does not contain the abietic acid that today distinguishes pine resin; neither does it contain agathic acid. Recently, however, it has been discovered that both extant and extinct species of the pine genus *Pseudolarix* produce succinic acid and its resin is chemically very similar to succinite (Anderson and LePage, 1995). The present day distribution of this genus is in Asia but included at least the Arctic during the Eocene. It may be highly significant that many Baltic amber inclusions have phylogenetic affinities with taxa today living in Asia (e.g., see summaries in Larsson, 1978). Baltic amber was likely produced by taxa related to *Pseudolarix* or even by an extinct species of this genus.

The Baltic amber forest was, obviously, not similar to those forests presently occurring in northern Europe. During the middle Eocene northern Europe was a single landmass. The remainder of the continent was composed of series of large central and southern islands or archipelagos in an expanded warm sea. This sea led northward into the Turgai Straits and Obik Sea that at the time separated Europe from northern Asia. Africa and India were still well separated from Europe and Asia, so most biotic exchange was between the latter two regions, although some connections were perhaps possible with North America earlier in the Paleocene and earliest Eocene (e.g., McKenna, 1975). Global climates in the Paleocene and Eocene were significantly warmer than in later Tertiary epochs. The climate in Europe in the Eocene was subtropical or tropical, probably very similar to present day pine forests in the South Atlantic Coastal Plain of

the United States (i.e., North Carolina to Florida).

During an era when human understanding wrestled vigorously with the idea of biotic and global changes, Rev. Hope (1836) had a profound insight into the biogeographical association of Baltic amber insects and the climate of the amber forest. Toward the conclusion of his paper summarizing, at the generic level, those taxa known to him in succinite he stated:

> From the above discrepancies I abstain at present from entering more largely into the geographical investigation of amber-insects, and reserve it for some future paper; but from what has already been adduced, may we not conclude that the climate and temperature of Europe have undergone considerable change? The above examples of tropical insects sufficiently testify that the amber-tree did not vegetate under a climate such as Prussia now enjoys, but in a warm region. I trust the above notices will afford a sufficient stimulus to induce others to take in hand a subject replete with interest; a subject embracing in its scope not only the changes of temperature and climate which our globe has undergone, but also the consideration of the geographical distribution of insects and plants, by which alone we can arrive at any satisfactory conclusion respecting them. (Hope, 1836: 137).

It is not of minor significance that Hope was able to make such broad-reaching conclusions concerning global change and zoogeography from even the most cursory study of Baltic amber inclusions.

The transition between the Eocene and Oligocene Epochs is a well-documented episode of extinction (e.g., Prothero, 1994). At this time global temperatures dropped precipitously and the geography of the world was significantly altered, particularly for Europe. As temperatures cooled dramatically toward the end of this epoch the tropical flora and fauna were gradually extinguished. Likewise, ocean levels and seaways were altered, bringing the European and Asian continents together and significantly shrinking the southern European ocean to create the Mediterranean Sea we are more familiar with today. Thus, those areas that were once tropical islands or subtropical mainland forests became part of a colder, more temperate, continual landmass and the "amber forest" disappeared.

MATERIALS AND METHODS

Many institutions throughout the world maintaining amber collections were contacted or visited regarding the presence of unstudied amber bees among their holdings and the possible location of lost types. Of the museums and individuals either contacted or visited I was only able to locate material in the following: **AMNH,** American Museum of Natural History, Division of Invertebrate Zoology, New York, New York, David A. Grimaldi; **BMNH,** The Natural History Museum (British Museum), Department of Palaeontology, London, United Kingdom, Andrew J. Ross; **BSPG,** Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany, Helmut Mayr; **GPUH,** Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Hamburg, Germany, Wolfgang Weitschat; **IMGP,** Institut und Museum für Geologie und Paläontologie, Göttingen, Germany, Hans Jahnke; **PMUZ,** Paläontologisches Museum, Universität Zürich, Zürich, Switzerland; **SAMH,** Swedish Amber Museum, Höllviken, Sweden, Leif Brost; **ZMHB,** Museum für Naturkunde, Institut für Paläontologie, Humboldt-Universität, Berlin, Germany, Erika Pietrzeniuk; **ZMPA,** Muzeum Ziemi Pan, Polska Akademica Nauk, Warsaw, Poland, Barbara Kosmowska-Ceranowicz; **ZMUC,** Zoological Museum, University of Copenhagen, Copenhagen, Denmark, Rudolf Meier. A single type specimen is deposited in Paris. Unfortunately, this material was not made available to me for study. The specimen is discussed below and the type depository abbreviated as follows: **MNHN,** Laboratoire d'Entomologie, Museum National d'Histoire Naturelle, Paris, France, Andre Nel.

In addition, specimens from the following personal collections were examined (material couriered through W. Weitschat, Geologisch-Paläontologisches Institut und Museum, Hamburg): **CCGG,** Collection of Carsten Gröhn, Glinde, Germany; **CDTG,** Collection of Dirk Teuber, Gütersloh, Germany; **CFEG,** Collection of Friedhelm Eichmann, Hannover, Germany; **CGHG,** Collection of Günther Herrling, Bramsche-Engter, Germany; **CFKG,** Collection of F. Kernegger, Ham-

burg, Germany; **CHFG,** Collection of C. and H. Hoffeins, Hamburg, Germany; **CHMG,** Collection of Hans Mendl, Kempten, Germany; **CJDL,** Collection of Jonas Damzen, Vilnius, Lithuania; **CJVG,** Collection of Jürgen Velten, Idstein, Germany; **CMGG,** Collection of Matthias Glink, Buxtehude, Germany; **CMSE,** Collection of Michael S. Engel, Lawrence, Kansas, United States; **CSUL,** Collection of Saulius Urbonas and Juozas Veilandas, Klaipeda, Lithuania. Although his material did not contain any bees (instead, spheciform and chalcidoid wasps), I am grateful to Horst Wegner (Hannover, Germany) for allowing me to examine specimens from his collections. To each of these collectors I am greatly indebted, particularly for their willingness to donate name-bearing types to museums (and therefore listed as belonging to particular museums herein).

Specimen Preparation and Study

When possible, specimens were vacuum-embedded in epoxy following the procedure of Nascimbene and Silverstein (2000). Water-fed trimming and polishing was then undertaken on most specimens so as to make clear "windows" for the observation of particular structures and photography. Amber pieces were then examined using a Zeiss Stereomicroscope SV-8 and measurements made using an ocular micrometer. Scanning electron microscopy was done on uncoated specimens using a Hitachi S4700 Field Emission Scanning Electron Microscope for partial inclusions of *Boreallodape striebichi* preserved at the amber surface (see below). I prepared a photographic slide of each specimen [a few of which are presented here as either color plates or black-and-white images (e.g., the frontispiece)], thereby creating a photographic library of bees in Baltic amber.

Format

In preparing this work the recently introduced fourth edition of the International Code of Zoological Nomenclature has been followed (ICZN, 1999b). Standard formats are used for taxonomic histories. References in each line refer only to taxonomic works and thus if a species was simply cited or listed by an author such a reference is excluded.

In presenting taxonomic summaries for family-group names only those names applicable to groups under consideration are presented. For example, under the subfamily Megachilinae the nominate tribe is not considered in the present monograph owing to the absence of this group from the Baltic amber fauna. The taxonomic history under Megachilinae therefore presents only the derivation of the family-group name based on *Megachile* and not all of the other names for valid tribes (e.g., Anthidiini, Dioxyini). Nor are synonyms of the nominate tribe included (in this particular example, synonyms of Megachilini, like Coelioxynae), since such synonyms are probably not equivalent with the group at a higher rank (e.g., in this work the family-group name based on *Coelioxys* should not be listed as synonymous with Megachilinae, since the former is not equivalent to a group inclusive of Anthidiini or other tribes of the subfamily but only with the Megachilini). The taxonomic history is presented only at its lowest rank within the family-group so as to avoid extensive repetition (e.g., the taxonomic history of the family-group name based on *Halictus* is presented under tribe Halictini and not also under Halictinae and Halictidae). For extant bees complete details on family-group names and their synonyms are presented by Michener (1986) with additions and corrections by Michener (1997) and Engel (1999e). A catalog of family- and genus-group names for fossil bees is presented in appendix 3, while a separate species catalog is in preparation (Engel, in prep.).

I have used the term *nomen translatum* for family-group names that have been changed in hierarchical rank (e.g., tribe elevated to subfamily) and required an alteration of suffix. The term *status novus* is reserved for changes in rank whereby the name retains its suffix from the former rank without alteration (e.g., subspecies elevated to species, subgenus elevated to genus). As stipulated by the Principle of Coordination (ICZN, 1999b: Art. 36), names altered in either manner retain their original authorship and date regardless of rank.

In the Material sections I have presented detailed label information from each specimen as well as a summary of the total num-

ber of specimens (immediately following the heading Material for each species). In these summaries a double slash (//) separates text from individual labels. The material sections are broken into paragraphs, with each paragraph representing a single amber piece except when the holotype and paratypes occur in the same piece; otherwise multiple individuals in a single amber block are treated within the same paragraph. Each paragraph is headed by a boldface indication as to whether this material is a type or not. When two or more taxa are synonymized there are two paragraphs with the boldface heading "holotype", "lectotype", or "neotype", but each is followed in parentheses by an indication as to which synonymous name it belongs. When the holotype for one species is the same specimen designated as the neotype for another, these begin separate paragraphs but are cross-referenced to avoid repeating label data.

As a result of attempting to forge a new path, I have had to make difficult decisions regarding previously described taxa for which specimens have since become lost or destroyed, mostly through the ravages of world war. I therefore found it necessary to designate neotypes and in so doing to carefully attempt to associate newer material with often inadequate and incomplete original descriptions. This has been done expressly for the purpose of stabilizing the nomenclature of fossil bees (in accordance with ICZN, 1999b: Art. 75.3.1) and thereby allowing and encouraging meaningful comparison of these taxa with Recent bees. For all of the taxa below I have provided necessary information for both the recognition of the specimens chosen as neotypes, my reasons for believing them to be conspecific with the original material, and diagnoses of all of these species (meeting the requirements of ICZN, 1999b: Art. 75.3.2, 75.3.3, and 75.3.5). Article 75.3.6 (ICZN, 1999b) states that the neotype must come "... as nearly as practicable from the original type locality."; since all of the original fossils, as well as my own, originate from middle Eocene strata of the Baltic region, I believe this criterion to have been sufficiently met. All neotypes are either in the AMNH, ZMHB, GPUH, or BMNH as indicated below, making them accessible for future study (satisfying ICZN, 1999b: Art. 75.3.7). The more difficult criterion to meet is Article 75.3.4, which requires reasons for "... believing the name-bearing type specimen(s)... to be lost or destroyed, and the steps that had been taken to trace it or them". All of the species for which neotypes were required were originally located in the Albertus Universität in Königsberg. During World War II the collections of this university were destroyed by fire. I contacted numerous institutions in search of described or undescribed material. The bulk of Königsberg's surviving material found its way into the collection of the Institut und Museum für Geologie und Paläontologie, Göttingen. I personally visited this institution during the summer of 1999 (as well as several other European collections) and inspected the entire amber collection. From this material I was only able to locate three original specimens (with Cockerell's own handwritten labels). I was therefore left with the conclusion that the remaining taxa, which could also not be traced in any other museum, must have been lost or destroyed during the tumultuous years of the last world war. For these reasons I believe to have adequately satisfied all of the ICZN (1999b) requirements, inclusive of Article 75.3.4, for the designation of neotypes.

Metrics are provided in the descriptions for the name-bearing type specimen. All measurements should be considered approximate, since it was not always possible to achieve the optimal angle for making a given measure. In the description of higher-rank groups, italicized characters indicate features that could not be confirmed for the fossils described within that particular group. The following descriptive abbreviations are used: F, flagellomere; OD, ocellar diameter (always based on the diameter of the median ocellus); S, metasomal sternum; T, metasomal tergum. Descriptions are of females (of the worker caste where applicable in the corbiculate Apinae) except for *Ctenoplectrella viridiceps* where a description of the male is included; otherwise males are unknown.

GENERAL MORPHOLOGY

Numerous accounts discuss the general external morphology of bees (e.g., Michener,

1944, 1965, 2000a; Snodgrass, 1956; Camargo et al., 1967; Urban, 1967; Eickwort, 1969; Pesenko, 1983; Engel, 2000a) and the ensuing section is not meant to entirely supplant those. Instead, I have attempted to summarize standard terms for the external morphology of bees, to relate each characteristic to gross variations found among the Baltic amber fauna, and to provide new terms for features not previously considered. This section is also intended to provide a working terminology for researchers and amateurs collecting, organizing, and studying Baltic amber inclusions. It is hoped that this overview of bee morphology will make the subsequent systematic section and its included descriptions and dichotomous keys more useful.

Morphological terminology generally follows that proposed by Michener (1944, 2000a) with additions for mandibular structure by Michener and Fraser (1978), coxal structure by Michener (1981a), and glossal morphology by Michener and Brooks (1984). From these accounts, however, I differ in some terminologies for wing veins, mouthpart structures, and leg structures most notably in terms used for types of pollen-carrying apparati (see specific instances below). The following sections provide greater detail into the precise morphology of bees in general and the Baltic amber bees in particular, defining terms frequently used throughout the text.

Prosoma

The head, or *prosoma,* is the first body tagma and is hypognathous. The *compound eyes* (figs. 1, 4) are situated laterally on the head and are composed of numerous minute facets representing the individual lenses of the ommatidia. At the top of the face, arranged in the pattern of an inverted triangle, are three simple eyes termed *ocelli* (fig. 1). At the extreme lower apex of the head is the *labrum* (figs. 1, 3), a freely movable sclerite that at its base broadly articulates with the remainder of the prosoma. The labrum is sometimes composed of two sections: the distal process and the basal area. The *distal process* (fig. 1) is a medioapical extension that extends apicad from the transverse *basal area* (fig. 1) and is slightly set below the plane of the basal area when viewed in profile; the basal area is the portion that articulates with the head capsule. When the distal process is present it is variously modified with either lateral teeth or serrations, a dorsal ridge or keel, or tubercles of differing morphologies. Similarly, the basal area can bear tubercles and/or ridges, and is found in a variety of gross morphological shapes, none of which depend on the presence or absence of the distal process. The labrum broadly articulates at the apical margin of the *clypeus* (figs. 1, 3), the lowermost, immovable sclerite of the head capsule. The basal attachment of the clypeus to the remainder of the head is delimited by the *epistomal sulcus* (fig. 1) (sometimes called the epistomal suture), which laterally forms an angle of various degrees of arc; typically the angle is measured between the two portions of the sulcus opening toward the compound eye. Similarly the dorsalmost, transverse portion of the epistomal sulcus ranges from convex (i.e., bending upward and extending the clypeus dorsally), straight, to concave (i.e., bending downward and shortening the clypeus). Almost universally (except in some living genera, such as *Nomioides*), the *anterior tentorial pits* are set into the epistomal sulcus, frequently along its lateral parts. Extending dorsally from the epistomal sulcus to the antennal sockets are the *subantennal sutures* (fig. 1). Typically there is a single subantennal suture reaching each antennal socket, although in some groups (e.g., Andrenidae) there are two subantennal sutures reaching each antennal socket and defining between them a small subantennal area. Frequently, the subantennal suture meets the antennal socket along its lower margin, although in the Lithurginae and Megachilinae the single subantennal suture runs to the outer, lateral margin (i.e., that side nearest the compound eye) of the antennal socket. The *antennal sockets* (or alveoli) (fig. 1) are the points at which the antennae articulate and, together with the subantennal sutures, serve to demarcate a poorly defined region of the head referred to as the *supraclypeal area* (figs. 1, 3). The face above the level of the antennal sockets to the level of the ocelli and between is the *frons* (fig. 1). The ill-defined region of the face running

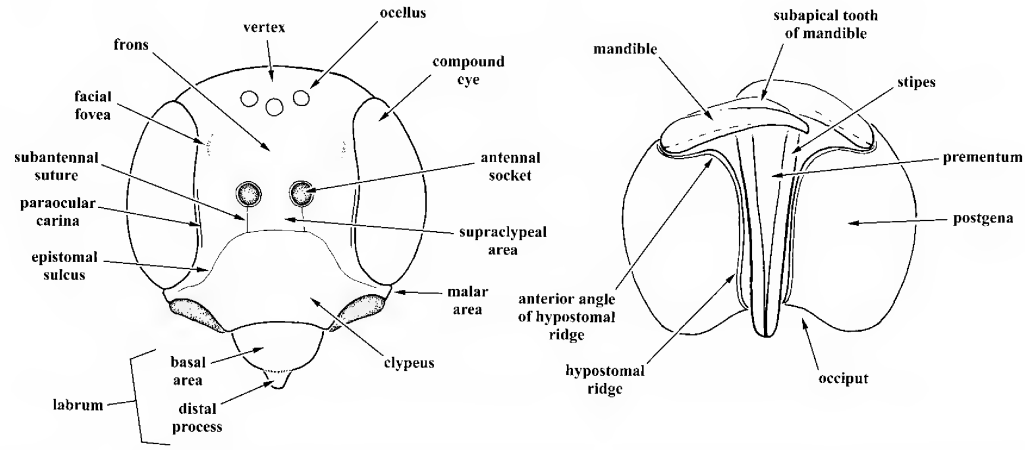


Fig. 1. Diagrammatic representation of a bee's head (= prosoma) with major morphological structures labeled. Left image is a frontal view of the head with the antennae and mandibles removed; right image is a ventral view of the head.

along the inner margin of the compound eye and outside of the frons is the *paraocular area,* which is sometimes equipped with a carina running dorsoventrally along the compound eye (i.e., the *paraocular carina*: fig. 1). In some bee lineages (e.g., Andrenidae) the paraocular area near the upper, inner margin of the compound eye bears a shallow integumental impression or *facial fovea* (fig. 1), sometimes covered with dense, microscopic setae. At the lower extremity of the compound eye is the *malar area* (fig. 1), a small region of integument separating the lower border of the compound eye from the mandibular articulation (see below). In some bee taxa there is an *interocellar furrow* formed of an impressed line running between and just posterior to the lateral ocelli (Engel, 1998b, 2000a). On the top of the head and immediately behind the ocelli is the *vertex* (figs. 1, 4), which runs to the posterior margin of the head where the head once again angles or curves ventrally to its posterior surface, or *occiput* (fig. 1). The ridge separating the vertex from the occiput is the *preoccipital ridge* (fig. 3) and surrounds the concave, posterior surface of the head (i.e., the occiput), which itself finally gives rise centrally to the *postocciput* that is surrounded by distinct *postoccipital sulcus* (or suture). The preoccipital ridge can be either rounded, angled, carinate, or even lamellate. The postocciput bears a large opening, the *foramen magnum,* where the prosoma and mesosoma connect. To the sides of the vertex the lateral portion of the head behind the eyes and ocelli and anterior to the preoccipital ridge is the *gena* (fig. 3), which ventrally gives way to the *postgena* (fig. 1) on the ventral surface of the head. The postgena borders a longitudinal concavity composed of the *hypostoma* on the undersurface of the head and is referred to as either the *hypostomal fossa* or the proboscidial fossa, since the proboscis (i.e., the labium and maxilla) rests within this region when in repose. The ridge separating the hypostoma from the postgena is the *hypostomal ridge* (fig. 1) and, like the preoccipital ridge, can be rounded, carinate, or even lamellate and frequently projects slightly beyond the occiput posteriorly. Anteriorly the hypostomal ridge curves laterally (fig. 1) and runs behind the mandibular articulation.

Articulating with the head are a number of appendages representing ancestral remnants of a once segmented, limbed tagma of a debated total number of somites. The appendages discussed here are not presented in order from anterior to posterior of their presumed relative position on ancestral segments. At the lower, apicolateral extremity of the head are the *mandibles* (figs. 1, 3). The mandibles of bees are variably structured and typically sexually dimorphic. Numerous an-

atomical details concerning mandibular structure were covered by Michener and Fraser (1978) and it is not necessary to repeat that material here. Instead, I shall focus on only those gross structural features that have been observed in the fossils discussed herein and require some explanation of their associated terms. The mandibles, as in all pterygote and some apterygote insects, are dicondylic, having two points of articulation and therefore moving in a single plane. The articulation is formed of an anterior mandibular acetabulum and a posterior condyle each corresponding to an anterior condyle and posterior acetablum on the head capsule, respectively. The apical margin of the mandible is frequently beset with a series of incisions defining apical teeth. Along the upper margin the *subapical tooth* (figs. 1, 3) and a groove (termed the *acetabular groove*) running from the mandibular acetabulum demarcate a region referred to as the *mandibular pollex,* while the remaining area of the mandible is the *rutellum.* The mandibular pollex is in some groups (e.g., the corbiculate Apinae) greatly expanded to form a single, elongate cutting margin, or is divided into additional teeth. On the outer margin of the rutellum are a series of ridges that delimit an associated number of interspaces. Along the lower margin of the mandile runs the *condylar ridge* (below it is the *condylar groove*) and between this ridge and the acetabular groove is the outer surface of the mandible with its *outer grooves,* the number and presence of which can vary among bee lineages (e.g., completely absent in some corbiculate Apinae, such as the honey bees).

The appendages of the next two head segments are intimately tied together and form the primary mouthparts of the bee. Frequently referred to as the proboscis or the labiomaxillary complex, these structures represent the *maxillae,* from the segment immediately behind that of the mandibles, and the *labium,* from immediately behind the maxillary segment, united basally by membranous connections which are typically strengthened anteriorly by thin, sclerotic *conjuctival thickenings.* The overall structure of the labiomaxillary complex as viewed from the front of a bee where the proboscis is fully extended (e.g., fig. 2) can be thought of as the lateral, paired maxillae and the central labium. The bases of the maxillae are the site of attachment and articulation of the labiomaxillary complex to the head capsule. The basalmost segment of the maxilla is the *cardo* (fig. 2), an elongate sclerite that attaches to the head capsule. At the apex of the cardo is the *stipes* (fig. 2), the next prepalpal segment of the maxilla, as well as the submentum (or lorum), the basalmost sclerite of the labium (see below). The ventral (lateral surface in fig. 2) margins of the stipes is sometimes concave with a distinct comb of stiff setae set within the concavity and termed the *stipital comb* (e.g., present in many Apidae). At the apex of the stipes is the frequently six-segmented *maxillary palpus* (fig. 2). Two sclerites form the postpalpal portion of the maxilla and are the elongate *galea* and the small *lacinia* (fig. 2). Like the stipes, the galea is frequently beset (in the short-tongued bee families) with a comb of stiff setae on its inner surface, which when present is referred to as the *galeal comb.* As mentioned above the basalmost sclerite of the labium is the *submentum* (fig. 2), which is often termed the lorum to indicate its dubious homology (Snodgrass, 1935) with the true submentum of other insects. As discussed elsewhere (Engel, 1999b), I prefer the term submentum as employed by Michener (1944) in place of lorum. The submentum is shaped like an inverted "V" in many bees (except in groups such as some Colletidae it is more of a broad inverted triangle, or in Halictidae, rectangular or membranous) with the apices of the submental arms meeting the cardines of the maxillae. Along the inner, subapical surface of the submental arm is sometimes a small spine referred to as the *submental spine* (fig. 2), most notably found in the corbiculate Apinae. Medially the submentum attaches to the *mentum,* a structure, sometimes absent or membranous, that at its opposite end meets the base of the *prementum,* an elongate sclerite (fig. 2). The apex of the prementum is trilobed with the lateral processes supporting the frequently four-segmented *labial palpi* and a more broad, *medioapical* (or *subligular*) *process* that varies in length (being either shorter or longer than the lateral processes) (fig. 2). Postpalpally on the labium are the lateral *paraglossae* and the medial

glossa (fig. 2). As is discussed briefly below (under Systematic Paleontology) the mouthparts of bees can be grossly classified into two structural categories: short-tongued and long-tongued. Most notably, in short-tongued bees the first two segments of the labial palpus are cylindrical and usually more or less equal in length to the distal two segments, while in long-tongued bees the basal two segments are greatly elongate and flattened. In short-tongued bees the glossa is frequently short (and, in the Colletidae, broadened or usually bilobed at its apex as in the spheciform wasps), while it is pointed and almost universally elongate in the long-tongued bees. The premental *fragmentum* is a detached basal portion of the prementum. This structure is involved in the articulation of the prementum with the mentum in melittid and other bees. In long-tongued bees the apex of the glossa bears a minute additional structure termed the *flabellum* (fig. 2). Numerous other characters of the labiomaxillary complex could be discussed at some length, but since they are hidden in most bee fossils, I will not treat them further here (but see Michener, 1944, 2000a; Snodgrass, 1956; Eickwort, 1969).

Lastly, the *antennae* are somewhat geniculate, bending at the pedicel, and, as mentioned above, articulate with the face above the level of the clypeus (figs. 3, 4). The antennae are composed of three units: a basalmost *scape* that articulates via a basal bulb with the antennal socket; a short, intermediary *pedicel*; and the typically filiform *flagellum* (rarely serrate in some odd, living genera), which is itself divided into a series of individual, cylindrical *flagellomeres* (figs. 3, 4), sometimes called flagellar segments. In bees the number of flagellomeres is dimorphic: females almost always having 10 and males 11. The relative lengths of the basal flagellomeres can be useful characters for separating groups of bees.

Mesosoma

The *mesosoma* is a combination of the true thoracic tagma with the first abdominal segment (= propodeum). It is thus composed of four primary segments: *prothorax, mesothorax, metathorax,* and *propodeum.* The meso- and metathoracic segments bear the wing articulations and are sometimes together referred to as the *pterothorax.* The major segmental structures are prefixed by "pro", "meso", or "meta" as a reference to which thoracic segment they relate (e.g., mesocoxa, metatibial spurs).

The *pronotum,* or dorsal surface of the first thoracic segment is expanded laterally to form lateral surfaces and processes (the *postcoxal processes*) that extend along the sides and behind the procoxae to form a complete or nearly complete ring tightly adjoining the anterior margin of the mesothorax (figs. 3, 4). Dorsally the pronotum extends somewhat laterally and is posteriorly broadly U-shaped; the shape of the *dorsolateral angle* (fig. 4), where the pronotum bends posteriorly, is a useful taxonomic character. Along the posterior border of the pronotal lateral surface and extending toward and just below the level of the mesothoracic wing base is a distinct *pronotal lobe* (fig. 3) that covers the first thoracic spiracle. The presence of this lobe is a synapomorphic trait of the superfamily Apoidea. As a result of this overall pronotal morphology the *propleura* face ventrally and lie anterior to the procoxae (fig. 3). The *prosternum* is mostly obscured from view between the propleura but can be viewed internally. The anterior, triangle-shaped apex of the prosternum has been termed by Snodgrass (1956) the *basisternum,* while the broad, posteriorly-projecting portion is the *furcasternum.* The overall shape of the prosternum varies among higher bee lineages (e.g., tribes). The lateral processes and apical extension of the basisternum are of varying lengths and the furcasternum is similarly variable, sometimes with a more or less developed longitudinal, medial groove. Most notable is the variation in construction exhibited among the corbiculate Apinae (e.g., Prentice, 1991) where, in the Apini and Meliponini, there is a strong constriction immediately posterior to the basisternum (i.e., between the basisternum and furcasternum).

The mesonotum, or dorsal surface of the mesothoracic segment, is divided into two primary units: the mesoscutum (or scutum) and the mesoscutellum (or scutellum). The *mesoscutum* is the larger, anterior sclerite the mesonotum (figs. 3, 4). It is laterally bor-

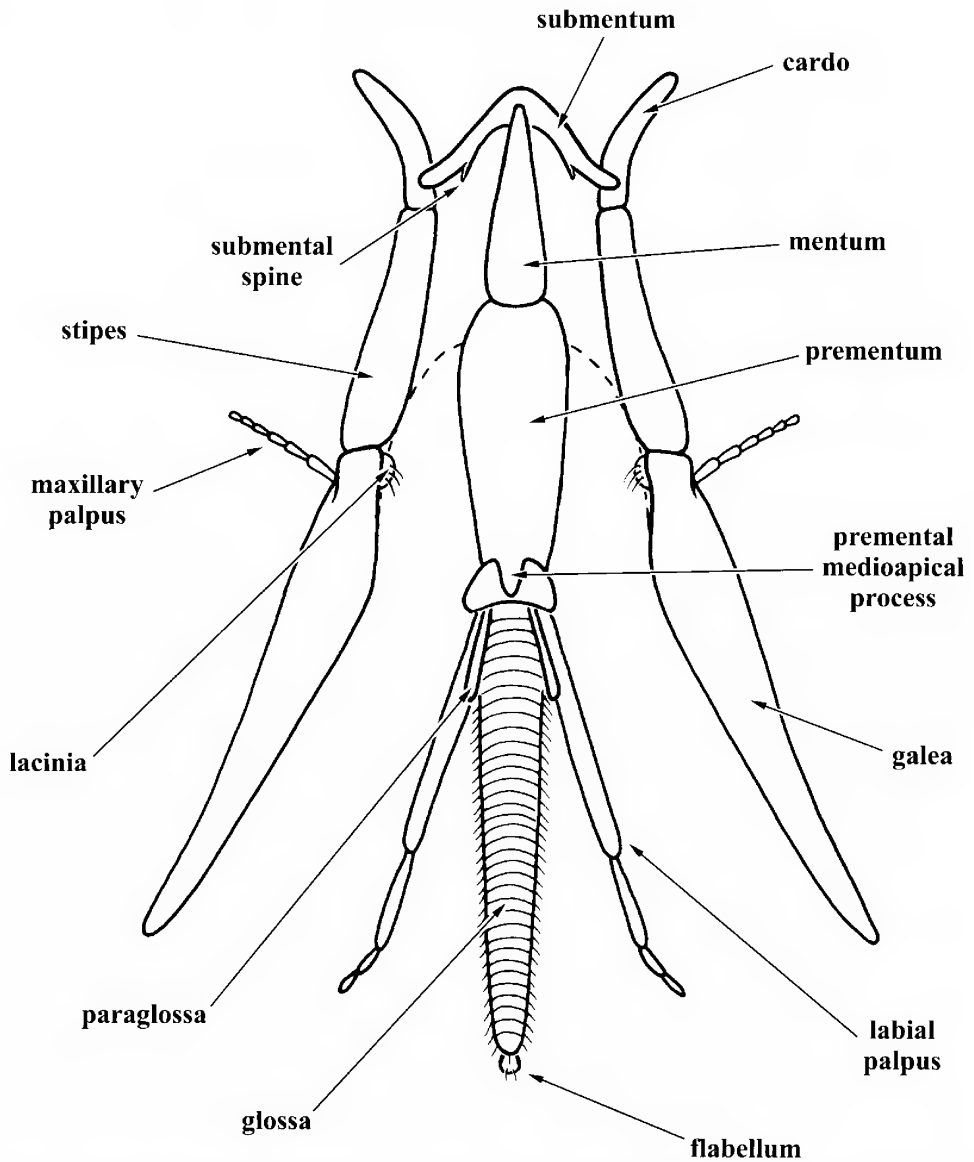


Fig. 2. Diagrammatic representation of a long-tongued bee's labiomaxillary complex with major structures labeled.

dered by small movable sclerites termed *tegulae* that cover the *mesothoracic wing bases* (figs. 3, 4). Borne upon the mesoscutum are a series of longitudinal, impressed lines. The *median line* (fig. 4), as the name implies, runs medially from the anterior border frequently to about the midpoint of the mesoscutum. The *notauli* are short, submedial lines that run from the anterior border to about one-third of the mesoscutal length in their most extreme case (fig. 4). The *parapsidal lines* are also parallel to the median line, although closer to the lateral, mesoscutal borders (fig. 4). Posterior to the mesoscutum is

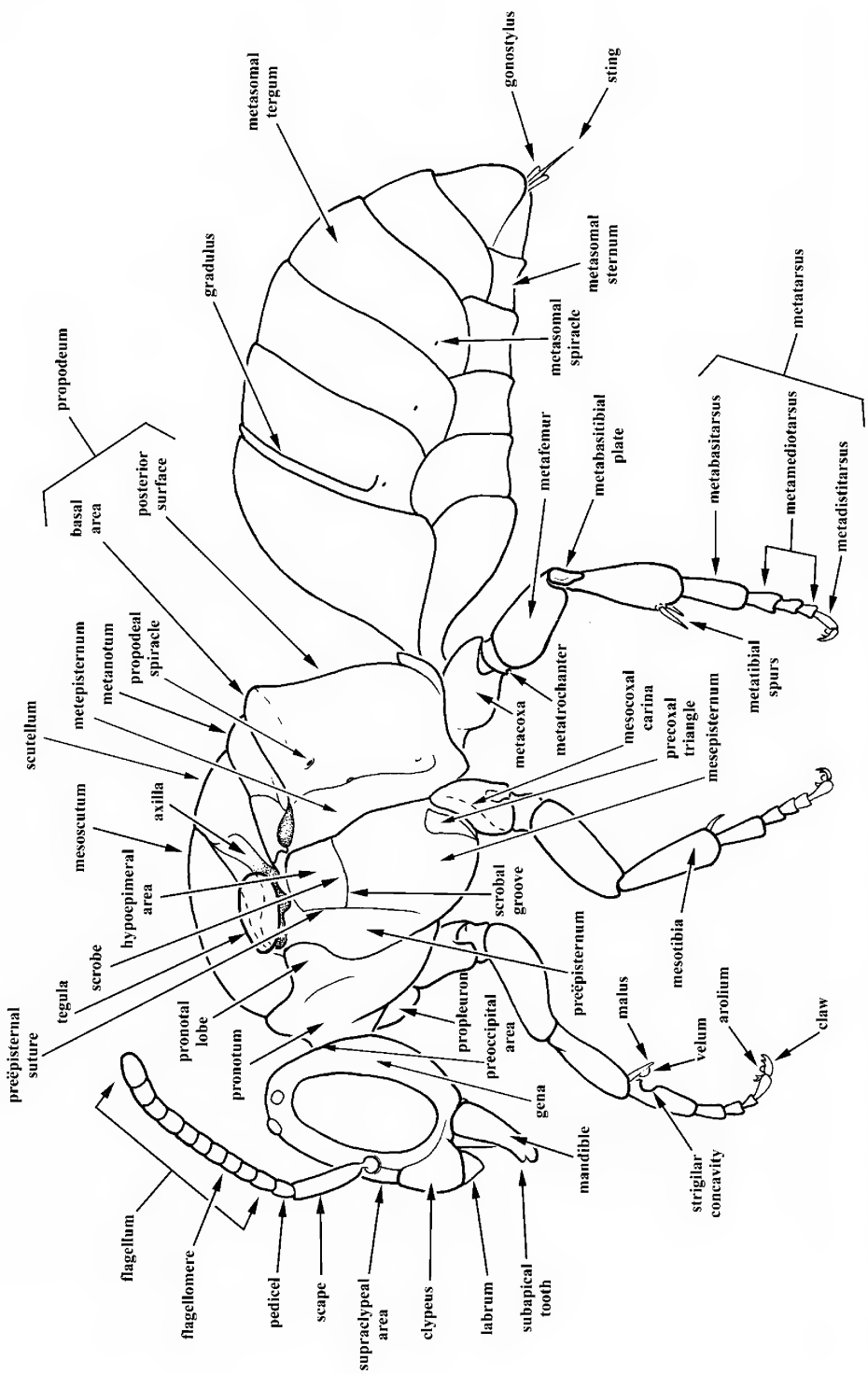


Fig. 3. Diagrammatic representation of a left lateral view of a bee with major morphological features labeled. NOTE: The figure combines characters not found in combination in any known bee (living or fossil); graduli not illustrated for all terga or sterna.

the *scutellum,* the second sclerite of the mesonotum (figs. 3, 4). The scutellum is frequently dorsally gently convex, while laterally it is concave and forms regions referred to as *axillae* (figs. 3, 4). The axillae are immediately posterior to the mesothoracic wing bases. The *mesepisternum* (figs. 3, 4) is the large, lateral portion of the mesothoracic segment. A series of ridges and grooves run across this surface and these structures are important characters for the recognition of suprageneric groups within bees. Running from just below the mesothoracic wing base toward the ventral margin is the *preëpisternal groove,* which serves to define the posterior border of a region termed the *preëpisternal area* or *preëpisternum* (fig. 3). If the mesepisternum is strongly bent, then the preepisternal area sometimes includes an anterior-facing surface. The preepisternal groove does not define the ridge separating this anterior-facing surface from the lateral surface of the mesepisternum; this ridge is termed the *omaular ridge* and can be rounded, carinate, lamellate, or rarely entirely absent. Running between the preepisternal groove and the posterior border of the mesepisternum is a short, longitudinal, impressed line that crosses a pit at about its midpoint. This pit is termed the *scrobe* or episternal scrobe, while the impressed line is termed the *scrobal groove* (fig. 3). Above the scrobal groove is a usually convex region of frequently distinctive sculpturing referred to as the *hypoepimeral area* (fig. 3). The *subpleural signum* is a small, impunctate, frequently raised spot at the separation of the pleural and ventral portions of the mespisternum. The *precoxal triangle* is a distinctive area of sculpturing on the mesepisternum bordering the mesocoxa in glyptapine bees (fig. 3). The precoxal triangle is delimited by a carina on all sides (posteriorly this carina is the precoxal carina). The integumental sculpturing within the precoxal triangle or the structure of its separation from the remainder of the mesepisternum is quite useful for separating species of the genus *Glyptapis.* The metathoracic segment is greatly shortened longitudinally by comparison to the mesothorax. Dorsally it is represented by the *metanotum* (figs. 3, 4) immediately posterior to the scutellum, which may sometimes project over its surface to varying degrees. Laterally the *metepisternum* (fig. 3) runs from the *metathoracic wing base* (fig. 4) to the metacoxa and typically narrows ventrally. As mentioned previously, the hindmost portion of the mesosoma is the *propodeum* (figs. 3, 4), which is ancestrally the first segment of the abdomen. The propodeum is frequently angled basally to form a dorsal-facing *basal area* and a *posterior surface* (figs. 3, 4). Typically, the sculpturing of the integument on the basal area of the propodeum is diagnostic for species or groups of species. Similarly, the angle between the basal area and the posterior surface can be useful for the definition of generic groups among bees. The *propodeal triangle* (= metapostnotum of Brothers, 1976) is a distinctive region of integument including the basal area or most of it and extending posteroventrally toward the *propodeal pit* (fig. 4) on the posterior surface.

The mesosomal appendages are all born on the true thorax. The legs are composed of the typical series of segments (from base to apex): *coxa, trochanter, femur, tibia, tarsus,* and *pretarsus*; the tarsus is further subdivided into the *basitarsus* (basalmost subsegment or tarsomere), *mediotarsus* (subsegments two through four), and *distitarsus* (distalmost subsegment) (fig. 3). The procoxae, like the propleura, are situated next to one another on the anteroventral surface of the mesosoma. The meso- and metacoxae are typically more well separated from one another, situated on the ventral surface of the posterior half of the mesosoma and closer to one another than either is to the procoxae. In most short-tongued bees families (i.e., Colletidae, Halictidae, Andrenidae) the mesocoxa is hemicryptic, that is to say its dorsal articulation is partially hidden inside of the mesosoma. All other bee families (i.e., Paleomelittidae, Melittidae, Megachilidae, and Apidae) have a fully exposed mesocoxa. The metacoxa is fully exposed and ventral to the metepisternum and anterior portion of the propodeum. The protrochanters are slightly laterally compressed segments that articulate in a longitudinal plane (rather than vertical plane of movement as in the meso- and metatrochanters). The femora and tibiae are elongate, tubular segments, typically widest at their midpoint. On the ventral, mediobasal surface of the

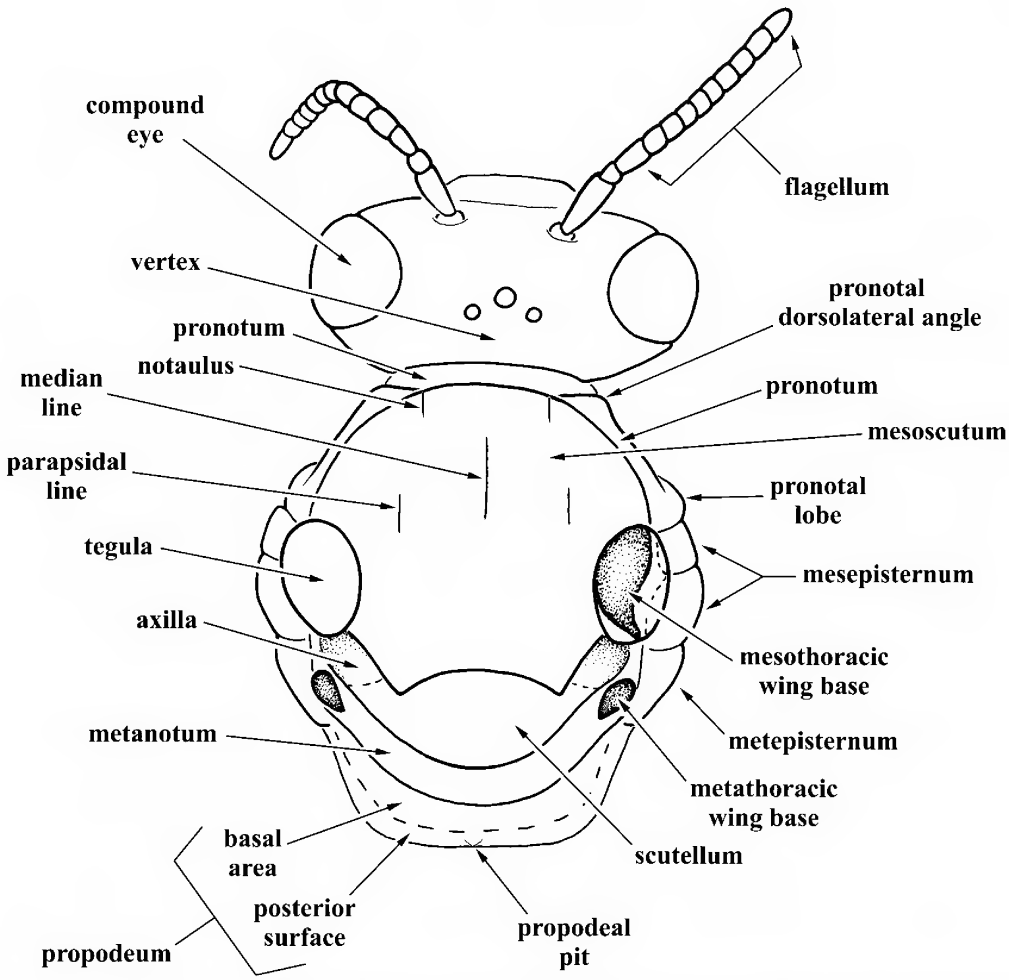


Fig. 4. Diagrammatic representation of a bee's prosomal and mesosomal dorsum with major anatomical structures labeled.

mesofemora is a dense, longitudinal series of short setae that form the *mesofemoral comb.* Similarly, on the inner, medioapical surface of the mesotibia is a dense, longitudinal series of setae termed the *mesotibial comb.* The metathoracic legs are typically modified for the transport of pollen (although this is by no means universal for bees; e.g., in Megachilidae pollen is carried on the metasoma). The *scopa* is developed to varying degrees and consists of elongate, frequently plumose setae on a variety of metathoracic leg segments of females except in parasitic species and the queen caste of some eusocial species. The leg segments bearing the scopal setae are useful characters for the separation of higher lineages among bees (e.g., in the extreme case the complete absence of scopal setae on the legs helps to characterize numerous parasitic taxa as well as groups such as the megachilids, where the scopal setae are born on the metasomal sterna). Thus, among bees there are metasomal scopae, femoral scopae, tibial scopae, &c. Perhaps the most distinctive pollen-carrying apparatus is the *corbicula* or "pollen basket" (fig. 5). The corbicula is

formed by an expansion of the metatibia toward its apex; it is somewhat flattened and the outer surface concave to varying degrees. The concave region on the outer surface (varying in length, although typically comprising only the apical half of the metatibia) is bordered anteriorly and posteriorly by elongate scopal setae. Michener (1999) has, as have some other authors (e.g., Thorp, 1979), used the term corbicula more inclusively for any glabrous, frequently concave surface bordered by fringes of elongate scopal setae and used for the transport of pollen. Thus some structures found in other bee groups (e.g., andrenines, halictines) may have what these authors refer to as "femoral corbiculae" or "propodeal corbiculae". In attempting to denote the uniqueness of the actual structure found only in the corbiculate Apinae, i.e., those taxa not only exhibiting the corbicula as defined by Michener (1999) but also the associated modifications of the metatibia, I prefer to restrict the term corbicula to this structure. Those other pollen-carrying apparati termed corbiculae by Michener (op. cit.), are here referred to as either corbiculate scopae or more appropriately as *fiscinae* (sing. *fiscina*: L. meaning "flower or bread basket"). Thus corbiculae s.s. are homologous structures found in a single clade of apine bees. Both scopae and fiscinae are more general terms for other pollen-carrying structures and are not necessarily homologous across taxa. Thus, it may prove at a later time to be useful to indicate such homologies by their own terms owing to the diversity of fiscinae among bees (e.g., the term "canistra" for a "propodeal fascina"). The inner surface of the metatibia of many bees and wasps is covered by a dense field of minute, blunt setae termed *keirotrichiae.* The region occupied by the keirotrichiae is termed the *keirotrichiate field* (fig. 5) and its separation from the remainder of the metatibial inner surface is a useful systematic character among Meliponini and Electrapini. Articulated on the inner apex of the tibiae are *spurs,* the number and general structure of which vary on legs of differing segments; there is a single protibial spur and a single mesotibial spur, while the inner apex of the metatibia ordinarily has two metatibial spurs (figs. 3, 5). The protibial spur is modified into part of an antenna cleaner or *strigilis* (fig. 3). The thickened, spur "backbone" of the strigilis is the *malus,* while along its inner basal margin is a broad lamella termed the *velum* (fig. 3). The overall shape of the velum does not vary greatly (typically it is roughly rectangular, but sometimes the outer margin of the lamella is slightly concave), although some corbiculate Apinae (e.g., Bombini, Electrobombini) there is a second anterior velum formed from a thickening along the anterior border of the malus and approximately orthogonal to the true velum; the anterior velum is not always developed into a lamella like the true velum. The distal portion of the malus that extends beyond the velum is either serrate, ciliate, or pectinate with a series of long teeth gradually decreasing in size apically. The mesotibial spur, while varying to some degree in length, is almost universally serrate or minutely ciliate. Among some living bee lineages there are other minor modifications of its apex, e.g., within Ericrocidini. The presence/absence or shape of the metatibial spurs varies dramatically among bee groups. In some lineages (e.g., the Meliponini and Apini) the spurs are entirely absent, while in several other groups a single metatibial spur is present (e.g., Electrapini, Melikertini). The spurs are typically of one of the three morphologies: serrate, ciliate, or pectinate; when two metatibial spurs are present the inner and outer spurs are not necessarily of the same morphological type. Along the inner, apical margin of the metatibia of corbiculate apines is a tight series of short, stiff setae known as the *rastellum* (fig. 5). In the Meliponini the outer surface of the corbicula near the posteroapical corner there is a *penicillum* (fig. 5), or dense patch of modified setae. As mentioned above, the tarsi are composed of five subsegments, the first of which is always greatly elongate by comparison to the distal four, and is referred to as the basitarsus. On the inner, basal surface of the probasitarsus is a deep concavity corresponding in relative position to the velum of the strigilis and serves as part of the antenna cleaning apparatus. This concavity is the *strigilar concavity* (fig. 3) and is frequently equipped with a linear series of fine setae to form a *strigilar comb.* The probasitarsus sometimes also bears a tight, longitu-

dinal series of setae referred to as a *probasitarsal comb*; non-homologous combs occur in a variety of positions and serve differing functions (e.g., Augochlorini, Tapinotaspidini). The mesobasitarsus is little different from the probasitarsus except that it lacks the stigilar concavity. The metabasitarsus is broader than the metamediotarsus and metadistitarsus, although the degree of its length-to-breadth ratio ranges dramatically across bee lineages. In some tribes of the corbiculate Apinae (i.e., Euglossini, Bombini, Electrobombini, Electrapini, Melikertini, Apini) the base of the metabasitarsus is modified into an *auricle* or pollen press (fig. 5). The auricle is formed of a slightly concave surface bordered by a carina or lip that is particularly broadly developed along the outer margin. The microsculpturing of this concavity is typically equipped with rows of microscopic, broadly flattened, pointed spicules directed toward the outer margin. The auricle, which is used to compress and move pollen into the corbicula for transport, is sometimes bordered along its outer margin by a series of more or less stiff setae here referred to as the *auricular basket.* The posterior apical or outer apical corner of the metabasitarsus is sometimes extended apically into a distal process beyond the articulation of the metabasitarsus to the metamediotarsus. This distal process sometimes bears a *penicillus* (not to be confused with the penicillum on the metatibia of Meliponini) or brush of dense, modified setae. The distatarsus is frequently slightly more elongate than the subsegments of the mediotarsus. The pretarsi bear the paired *claws,* which themselves sometimes bear an inner notch of varying depths to form an inner tooth (fig. 3). Toothed claws occur in most bees, although some lineages (e.g., Megachilini) have simple claws. Between the claws is a membranous lobe or *arolium* (fig. 3), the presence or absence of which is an important character for distinguishing taxa in a variety of lineages. A number of other associated structures are present in the protarsus [these are covered in greater depth by Michener (1944)]; none of these structures were observed for the Baltic amber bees (owing to their minute size and optical limitations).

The wings are borne on the meso- and metathoracic segments and are joined to the mesosoma via a series of complex, minute *axillary sclerites.* For further details on the morphology of the axillary sclerites in bees refer to Michener (1944) and Snodgrass (1956). The wings are formed of a membrane braced by longitudinal, sclerotic veins (abbreviated by capital letters) that are themselves, when not fused, connected at various points by transverse crossveins (abbreviated by lowercase letters). At the wing base the longitudinal veins in the forewing are (from anterior to posterior: fig. 6) the *costa* (C), the fused *subcosta* and *radius* (Sc+R), the *media* fused with the *cubitus* (M+Cu), and the first *anal* (A); the radius further out in the wing splits to form a posterior branch termed the *radial sector* (Rs). At roughly one-third of the total forewing length from the base, the media and cubitus separate and follow separate courses, the former eventually fuses for a short distance with the radial sector before separating once again shortly thereafter (fig. 6); the first abscissa of M (the free portion of this vein immediately after its separation from Cu) is termed the *basal vein.* In the hind wing the longitudinal veins are *Sc+R* (the costa is lost in the hind wing, leaving an unbraced, membranous leading edge), *M+Cu,* and *A.* Along the leading edge of the forewing there is an enlarged, sclerotized region (that weighs the leading edge of the wing) termed the *pterostigma* and formed of an expansion in R. Immediately basal to the pterostigma is a region formed of an expansion of Sc+R termed the *prestigma.* The basalmost edge of the prestigma is defined by the point at which the first abscissa of Rs originates from Sc+R. The leading edge of the hind wing is equipped with a series of minute hooks termed *hamuli* (fig. 7), which link the two sets of wings in flight. The number and pattern of arrangement of the hamuli is variable across bee taxa and is a useful taxonomic character. Crossveins are denoted by two letters indicating which longitudinal veins they connect; anterior vein first, posterior second (i.e., rs-m runs between Rs and M). Sections of the longitudinal veins running between two crossveins are termed *abscissae* and are numbered from base to apex; similarly, when more than one crossvein occur between a pair of longitudinal veins they

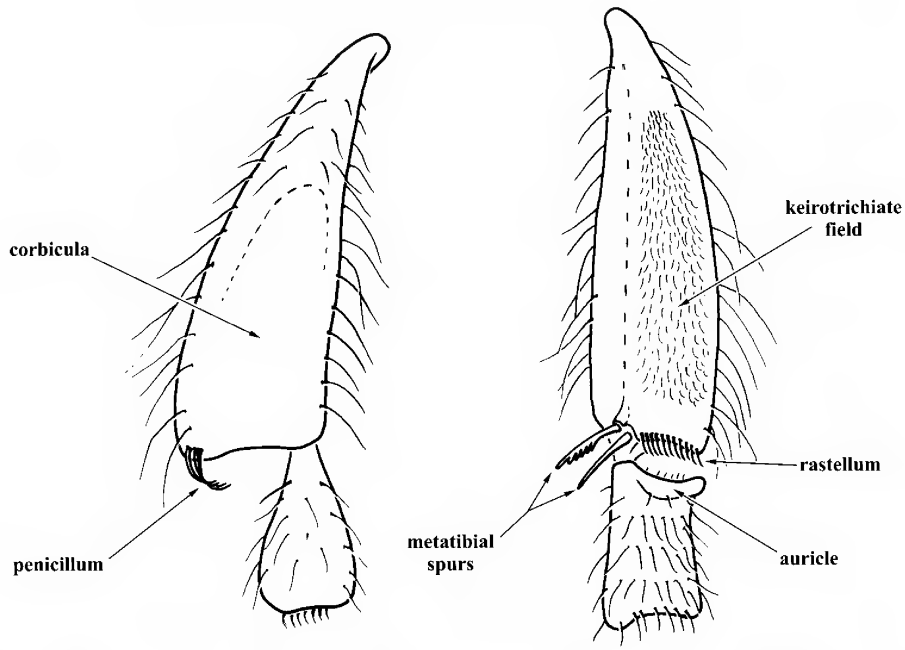


Fig. 5. Diagrammatic, corbiculate metatibiae with structures labeled. Left metatibia depicts an outer surface; right metatibia depicts an inner surface. NOTE: The figured metatibiae are not meant to represent outer and inner surfaces of the same leg or a single species.

are numbered consecutively from base to apex and this number precedes the crossvein abbreviation (e.g., 2m-cu). At specific locations certain veins are crossed by minute clearings of sclerotization termed *alar fenestrae* that indicate flexion lines where the wing will bend or fold during the motion of flight. Some of these lines are indicated in wing illustrations by dotted lines crossing the submarginal cells and their associated veins. Fusion and confusion would be an appropriate descriptor for the pattern of veins in the Hymenoptera forewing and its changes through the evolutionary history of the order. It would be excessive to discuss at length every point at which two veins merge, separate, remerge, and eventually terminate. Thus, for the sake of brevity, I refrain from such a discussion here and refer the reader to figure 6 where all of the veins are labeled. It must be noted that some of the vein terms used here differ from other works on bees. I have attempted to standardize the wing vein terms of the Apoidea with general work on the order so as to indicate the homologies of these veins not only among superfamilies of Hymenoptera but, as best as can be done, across insect orders. A few of these differences are as follows: **1.** the *anal vein* is often referred to as the vannal vein (abbreviated as "V") in other works on bees; **2.** those veins delimiting the apical edge of each submarginal cell and often referred to as the transverse cubitals (despite having no association with the cubitus!), or more appropriately the submarginal veins (referred to as transverse submarginals in Michener, 2000a), are considered to be herein, from basal to apical, the *second abscissa of Rs, 1rs-m,* and *2rs-m* (when only two submarginal cells are present these veins are second abscissa of Rs and 2rs-m; see below), respectively; in other accounts where the vernacular terms are not employed the indication that the latter two crossveins arise from Rs is dropped and they are termed 1r-m and 2r-m; **3.** in a similar fashion the small crossvein running between the pterostigma (R) and the posterior border

of the marginal cell (formed of Rs) just beyond the first submarginal cell is actually the *r-rs* crossvein but is frequently and enigmatically referred to as simply "r", presumably owing to the fact that this crossvein runs between two portions of the radial system; **4.** in the hind wing the crossvein r-m is changed to *rs-m* to regain, once again, more information pertaining to which section of the radial system this vein connects to the medial system. Thus, although these are minor alterations to the terminology of bee wing veins, they more accurately reflect the identity of the veins as they are presently understood and refer to homologies outside of the Apoidea. The membranous regions of the wing running between the veins are termed cells when bounded on all sides by veins. The cells of the forewing and hind wing are indicated in figure 7. I will mention only two sets of cells that play a particularly important role in the following descriptions and keys. The *marginal cell* is the large membranous region apicad the pterostigma and bordered by R anteriorly and r-rs and Rs posteriorly. This cell is variously modified, particularly at its apex, which can be set along the leading edge of the wing, bent away from the leading edge of the wing to different degrees, become broadly truncated (e.g., Perditini, some Electrapini), sometimes equipped with a minute abscissa of Rs beyond the cell (the cell is referred to as appendiculate when this abscissa is present: e.g., fig. 7), or in the most extreme case be entirely open (e.g., the stingless bees: figs. 111, 113). The *submarginal cells* are a longitudinal series of two or, more frequently, three cells immediately posterior to the pterostigma and marginal cell; when only two cells are present it is typically owing to a loss of 1rs-m, thereby effectively uniting the second and third submarginal cells. The shapes and and relative sizes of the submarginal cells are useful for distinguishing species and genera of bees. In one of the most extreme instances (i.e., the forewing of some Meliponini) the loss of the distal wing veins has left not only the marginal cell open at its apex, but the submarginal cells are completely lost (e.g., figs. 111, 113). The posterior edge of the membrane of the wings is typically incised at specific sites that indicate the endpoints of particular folds in the wing. These incisions and furrows demarcate specific regions of the insect wing that appear as lobes along the posterior edge of the wings. The basalmost lobe is the *jugal lobe* (fig. 7), which defines the anterior border of that region of the wing termed the *jugum.* The absence, presence, and size of the jugal lobe in the hind wing is a useful character for recognizing groups of bees. This structure, however, can be easily misinterpreted even in living bees since the jugal lobe frequently folds under the remainder of the hind wing and therefore appears absent. In fossil bees this is even more problematic since the amber often makes it difficult to discern the margins of such a folded lobe when attempting to look through the membrane of the wing; this is further complicated by the fact that amber sometimes has a "clearing" effect on wing veins and membrane, making them appear more faint. The next more apical lobe is the *vannal lobe* (fig. 7) and is defined by a fold running near to the anal vein; the region between the jugal fold and the vannal fold is the *vannus.* The vannus is the posterior part of a region typically termed the clavus among other groups of Hymenoptera and other insects; the associated structures are referred to in those instances as the claval lobe and claval furrow (the latter of which typically runs just posterior to Cu). Thus, in other groups of Hymenoptera what is referred to in bees as the vannal lobe is sometimes termed the claval lobe. The remainder of the wing membrane apical from the axillary region (bearing the axillary sclerites) is the *remigium.* The lobes of the hind wing are particularly useful for classifying bees. The relative sizes of the jugal and vannal lobes as well as the presence or absence of the former are useful phylogenetic and taxonomic characters. Because they are rather uniform, those lobes of the forewing are not typically referred to for classificatory purposes, but the vannal lobe, at the minimum, is present. The membrane of the wings is typically covered by minute setae, although in some bee groups (e.g., *Xylocopa, Bombus, Electrobombus*) the apical portion of the wing beyond the veins is studded with minute, darkened swellings termed *alar papillae* (labeled as such in fig. 6). The

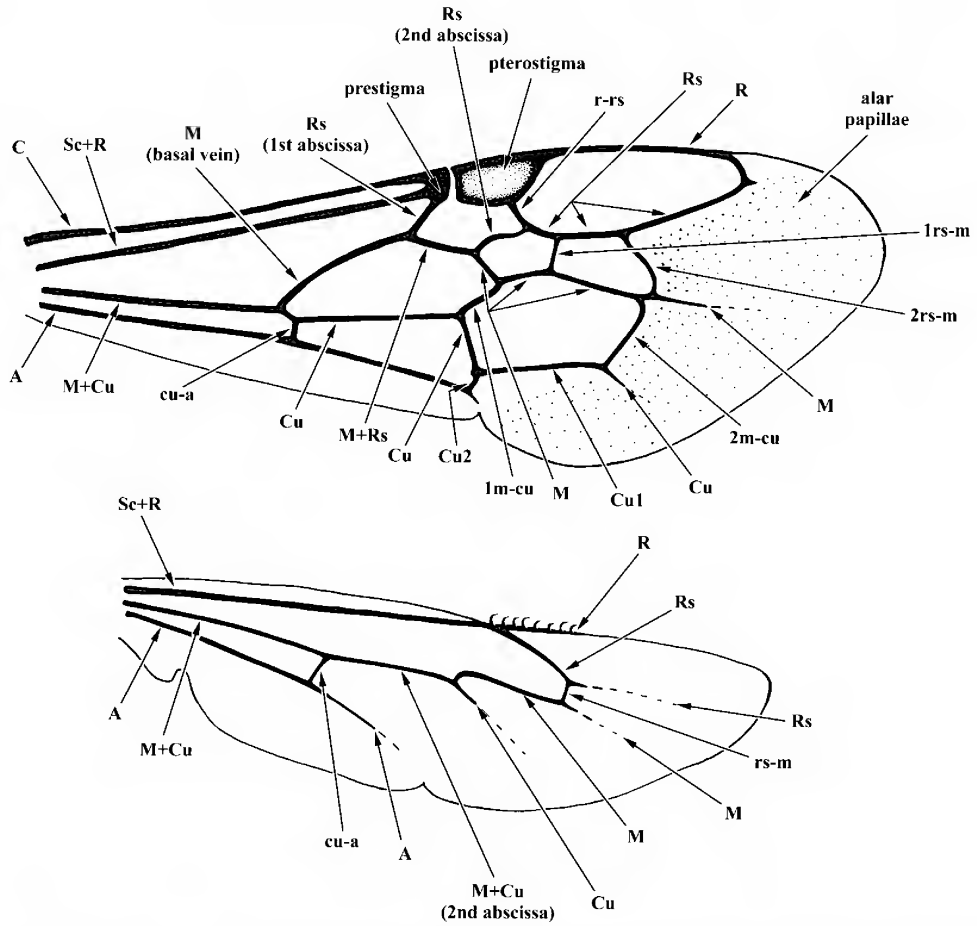


Fig. 6. Diagrammatic wing with longitudinal and crossveins labeled as well as a single membrane feature (i.e., alar papillae). Upper image is a forewing; lower image is a hind wing.

wing membrane is usually hyaline but can be infuscated or patterned to varying degrees.

Metasoma

The metasoma consists of the true abdomen minus the first segment that is fused to the thorax. Each of the metasomal terga and sterna has a suite of morphological structures associated with them, but are not discussed further here since they are almost universally unobserved for the known fossil bees. For a more complete discussion of the exoskeletal morphology of the metasoma refer to Michener (1944, 2000a), Snodgrass (1956), and Eickwort (1969), among other authors. The first metasomal tergum is constricted anteriorly to join the mesosoma and is therefore typically composed of an anterior-facing surface as well as a dorsal-facing surface. In the Lithurginae the first tergum is shortened such that there is no dorsal-facing surface. Running transversely across the basal half or the middle (or basal part of the visible portion of terga and sterna) of each tergum and sternum at about the level of the spiracle is a distinct line that is frequently carinate or minutely lamellate, referred to as the *gradulus* (fig. 3). The gradulus divides the terga and sterna into *pregradular* and *postgradular* regions.

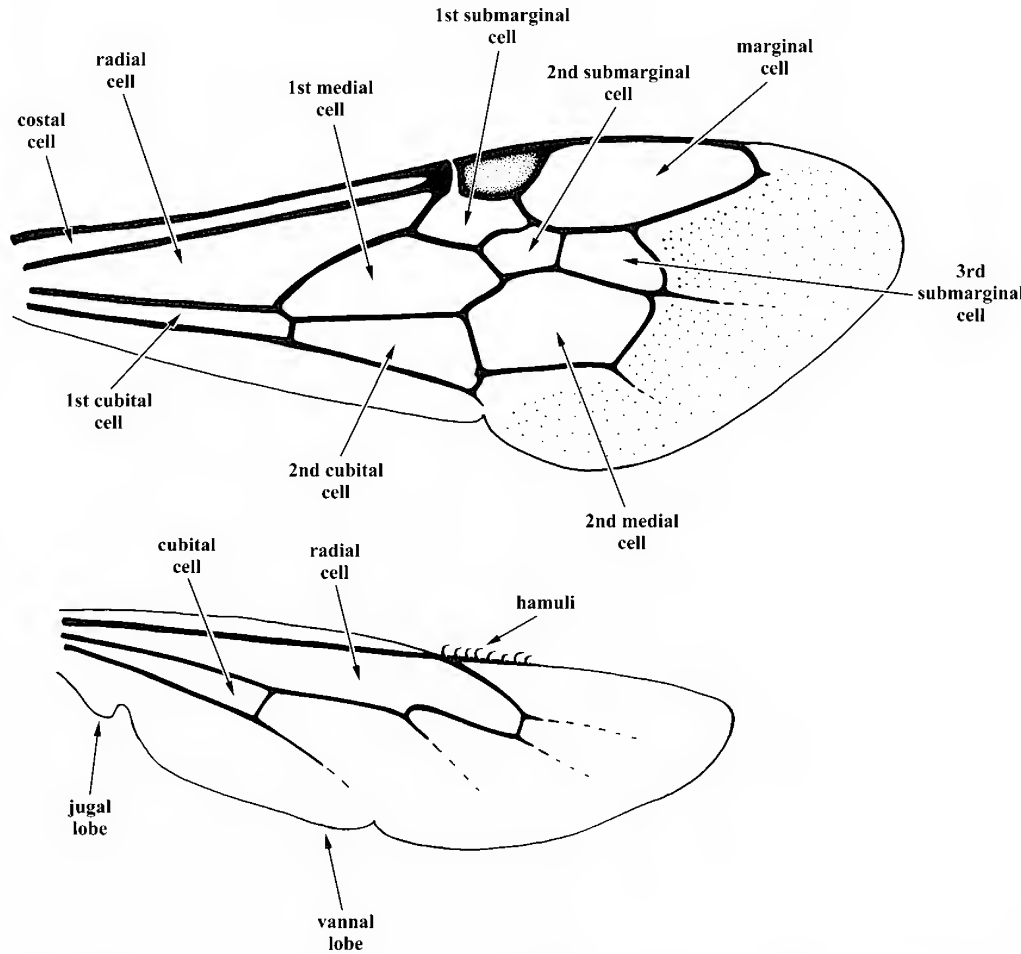


Fig. 7. Diagrammatic wing with membranous cells and gross anatomical structures labeled. Upper image is a forewing; lower image is a hind wing.

The terminalia (i.e., sting apparatus, male genitalia) of bees is not considered in the present work simply owing to the fact that in no Baltic amber bee specimen are these structures visibly preserved (except the sting apex in many individuals and with less frequency the worker gonostyli). The sting is the modified ovipositor of female Aculeata (fig. 3), while the female gonostyli, or sting sheaths, are what are typically referred to as the third valvulae (which themselves are the apical accessory lobes or styli of the second valvifer: see Snodgrass, 1935; Michener, 1944). For information on terminal structures, particularly those of the male, refer to Snodgrass (1935, 1941, 1956), Michener (1944, 1965, 2000a), or Eickwort (1969), among other publications.

SYSTEMATIC PALEONTOLOGY

This section covers the descriptive morphology and taxonomy of all bees presently known in Baltic amber. Numerous keys are presented, all of which apply only to those groups presently known from Baltic amber. Therefore, in each case the reader should not be alarmed at the exclusion of certain taxa

(e.g., the absence of Colletidae from the key to families of bees, for this family is not currently known from the middle Eocene of Europe). Likewise, characters are employed that may only apply to certain groups of a particular family if those particular groups are the only ones presently known in Baltic amber. For example, the strongly arcuate basal vein is given as a character to separate Halictidae in the key to families, because only the subfamily Halictinae is presently known in Baltic amber, even though the subfamilies Rophitinae and Nomiinae lack this feature. Similarly, within Apidae, only corbiculate apines are presently known in Baltic amber and so the key to subfamilies of Apidae uses the presence of a corbicula to separate Apinae from Xylocopinae, even though numerous living tribes of Apinae also lack a corbicula. Thus, future researchers discovering bees in Baltic amber should be careful when using these keys, since new specimens may represent higher rank groups (e.g., the aforementioned Colletidae) that would be new records for Baltic amber and were unknown to me at the time of this study. Naturally, I would be interested in examining any newly discovered fossils for the preparation of future supplements to this monograph.

Superfamily Apoidea Latreille

Diagnosis: Aculeate Hymenoptera macropterous in both sexes; sexual dimorphism slight. Antenna with 10 flagellomeres in females and 11 in males (except in a few, apomorphic instances). Posterior border of pronotal lateral surface extended just below level of wing base to form a distinct pronotal lobe; postcoxal process of pronotum greatly produced mesad and approaching counterpart (processes well separated in most spheciforms, while being much closer, if not in contact, in bees); posterodorsal margin of pronotum broadly U-shaped. Prepectus transverse and fused midventrally to mesopleurosternum. Metapostnotum ("propodeal triangle") expanded, fused to propodeum. Forewing with well-developed venation, frequently with 9 to 10 closed cells; hind wing frequently with jugal lobe. Metasomal S1 and S2 not separated by a strong constriction. Ovipositor concealed at rest and modified as sting.

TABLE 4
Familial Classification of Superfamily Apoidea

SUPERFAMILY APOIDEA LATREILLE
"Division Spheciformes"
†Family Angarosphecidae Rasnitsyn
Family Heterogynaidae Nagy
Family Ampulicidae Shuckard
Family Sphecidae Latreille
Family Crabronidae Latreille
"Division Apiformes"
Family Colletidae Lepeletier de Saint Fargeau
Family Halictidae Thomson
Family Andrenidae Latreille
†Family Paleomelittidae Engel
Family Melittidae Schenck
Family Megachilidae Latreille
Family Apidae Latreille

† Extinct.

Comments: The superfamily Apoidea consists of two primary divisions: the paraphyletic assemblage of spheciform wasps (families Angarosphecidae, Ampulicidae, Crabronidae, Heterogynaidae, and Sphecidae), and the monophyletic bees (Apiformes). The "Spheciformes" is not treated further herein. Table 4 summarizes the familial classification of the superfamily.

It has been observed that the name Spheciformes is a hybrid name (composed of Greek *sphekos* and Latin *forma*) and should therefore be replaced by appropriately formed names; namely Sphecomorpha (= Spheciformes) and Melissomorpha (= Apiformes). I have chosen to follow Brothers (1975) for these informal groups rather than employ those terms of wholly Greek origin.

Key to Divisions of Apoidea

1. Body setae simple; metabasitarsus not broader than remaining tarsal segments, frequently with strigil; female T7 not divided into hemitergites ..... "Spheciformes"
– At least some setae, particularly those of legs and surrounding propodeal spiracle, branched or plumose; metabasitarsus flattened, wider than remaining tarsal segments, without strigil; female T7 divided into hemitergites (bees) ..... Apiformes

Division Apiformes (The Bees)

Diagnosis: Some setae branched or plumose; subantennal sutures internally connected to fan-shaped sheet of tentorium; labrum thickened basally and attached at clypeal margin; proboscidial fossa opened onto posterior surface of head capsule; cardo not broadened apically, approximately parallel-sided; suspensorium of paraglossa with sparse setae or bristles; mesotibial comb present; dorsoventral length of mesocoxa about equal to distance from summit of mesocoxa to hind wing base; metabasitarsus broader than following tarsal segments, without concavity or strigil; cu-a of hind wing shorter than second abscissa of M+Cu; T7 of female divided into two hemitergites.

Comments: The bees are a monophyletic group among the Apoidea. Although I have not included it in the list above, an additional character diagnosing the bees includes the vegetarian diet of the larvae. Aside from a few, apomorphic exceptions bee larvae consume pollen, nectar, and plant oils.

McKenna and Bell (1997: 513) presented a series of ranks and suffixes for family-group names (adapted from Bour and Dubois, 1984) that could be applied to provide more hierarchy to the classification of Apoidea. In particular the rank of epifamily (intermediate between superfamily and family and with suffix *-oidae*) could be applied to refer to the bees as a whole. This would result in what I have called division Apiformes being replaced by epifamily Apoidae. Since this name would be quite similar to the superfamilial name (i.e., Apoidea), I feel that it would merely lead to confusion with the more inclusive group consisting of the spheciforms and bees. I have, therefore, used informal names without official ranks for these intercalary entities.

Short-Tongued Versus Long-Tongued Bees

Bees have been segregated into major groups; or the short- and long-tongued bees, a division originally recognized by Kirby (1802) and used ever since. Although these vernacular names are useful, they are a bit of a misnomer as these characters are not universal (also, one is a paraphyletic group). The long-tongued bee families (Megachilidae and Apidae) have the first and second segments of the labial palpus sheath-like (i.e., elongate and flattened), while short-tongued families (Colletidae, Halictidae, Andrenidae, Paleomelittidae, and Melittidae) have these same segments cylindrical and more or less similar to the following segments. The long-tongued families have been repeatedly demonstrated to be a monophyletic group; the short-tongued families are not. The short-tongued family Melittidae, in particular, has been demonstrated to be more closely related to the Megachilidae + Apidae clade owing to the shortened jugal lobe, fully exposed mesocoxa, and V-shaped submentum, among other characters. Michener and Greenberg (1980), for the purposes of a discussion on the higher-level phylogeny of bees, subdivided these groups so as to reflect the special position of Melittidae among short-tongued bees. Most notably these authors distinguished "basic short-tongued bees" apart from "short-tongued bees" (as well as other phenetic groupings not employed here). In the following text I regularly refer to these entities for comparative purposes. It therefore seems worthwhile to briefly provide a definition of these terms.

Long-Tongued Bees (= Megachilidae and Apidae): families with elongate and flattened labial palp segments one and two; jugal lobe shortened; mesocoxa fully exposed; submentum V-shaped; preëpisternal groove absent at least below level of scrobe.

Short-Tongued Bees (= Colletidae, Halictidae, Andrenidae, Paleomelittidae, and Melittidae): families with cylindrical labial palp segments one and two. Among this group the Melittidae stand out by having the short jugal lobe, V-shaped submentum, absence of the preepisternal groove; and fully exposed mesocoxa typical of the long-tongued bees. Paleomelittidae is also noteworthy in that it has the characters of the basic short-tongued bees (defined below) except this family has a fully exposed mesocoxa and lacks a preëpisternal suture (like Melittidae and long-tongued bees) but retains the elongate jugal lobe.

Basic Short-Tongued Bees (sensu Michener and Greenberg, 1980: = Colleti-

dae, Halictidae, and Andrenidae): families with cylindrical labial palp segments one and two; jugal lobe elongate; mesocoxa hemicryptic; submentum plate-like; preëpisternal groove complete.

Key to Families of Bees in Baltic Amber (Based on Females)

1. Scopa strongly developed on metasomal sterna; subantennal sutures directed to outer margins of antennal sockets (figs. 26, 32, 40); long-tongued bees . . . . . Megachilidae Latreille
– Scopa not developed on metasomal sterna, variously developed on hind legs; subantennal sutures attaching to antennal sockets on inner or lower margins (e.g., figs. 12, 17, 21, 49, 59, 64); short- or long-tongued bees 2
2. Preëpisternal groove absent below level of scrobe; mesocoxa fully exposed; basal vein variously shaped; short- or long-tongued bees 3
– Preëpisternal groove present and complete; mesocoxa hemicryptic; basal vein strongly arcuate (fig. 13); basic short-tongued bees . . . . . Halictidae Thomson
3. Jugal lobe of hind wing short (e.g., figs. 63, 76); flabellum absent or present; preëpisternal groove either present or absent; short- or long-tongued bees 4
– Jugal lobe of hind wing elongate; flabellum absent; preëpisternal groove absent below level of scrobe; short-tongued bees . . . . . Paleomelittidae n. fam.
4. Short-tongued bees (i.e., labial palp segments one and two cylindrical and similar in length to distal segments); flabellum absent; galea not elongate or if elongate then prepalpally, galeal comb present . . . . . Melittidae Schenck
– Long-tongued bees (i.e., labial palp segments one and two elongate and flattened); flabellum present; galea elongate postpalpally, galeal comb absent . . . . Apidae Latreille

Short-Tongued Bees

Family Halictidae Thomson

Diagnosis: The halictids comprise three homogeneous subfamilies of basic short-tongued bees (i.e., cylindrical labial palp segments, elongate jugal lobe, hemicryptic mesocoxae, &c.; see above). Halictidae is most notable for the loss of the mentum and submentum.

Description: Subantennal suture meeting inner, lower margin of antennal socket, infrequently lower margin; two subantennal sutures in some Rophitinae otherwise only one subantennal suture present (only one in the known fossils). Facial foveae typically absent. *Galea elongate prepalpally. Mentum and submentum absent*; segments one and two of labial palpi similar to distal segments, cylindrical, rarely elongate; glossa acute, typically short, without flabellum. Preëpisternal groove complete (except in Nomiinae groove weak or absent below scrobe). Mesocoxa with exposed area shorter than distance from summit to metathoracic wing base; metabasibitial plate frequently present (except in parasitic forms); scopa developed on hind leg in nonparasitic females. Jugal lobe of hind wing much more than half as long as vannal lobe. Pygidial plate present in females. *Volsellae present.*

Comments: The family presently contains three subfamilies: Rophitinae, Nomiinae, and Halictinae. The monophyly of the rophitines remains to be tested and the subfamily is possibly paraphyletic. The Nomioidinae sensu Alexander and Michener (1995) and Michener (2000a) is considered here as the basal tribe of Halictinae (see also Engel, 2000a; Pesenko, 1999; Pesenko et al., 2000). Of these subfamilies, only the Halictinae is presently known from the fossil record.

Subfamily Halictinae Thomson

Diagnosis: This subfamily is most closely related to the Nomiinae, both sharing the development of the scopa on the metafemur (rather than the metatibia in Rophitinae), the distal process of the labrum (absent in Rophitinae), and strong distal process with a penicillus on the metabasitarsus (either completely absent or under-developed in the basalmost subfamily, Rophitinae). The halictines can be separated from the nomiines most notably by the third submarginal cell being shorter than the first submarginal cell, by the prepygidial fimbria being typically divided by a longitudinal median line or area, and by the complete and strong preepisternal groove.

Description: Labrum of female with distal process. Clypeus longer than labrum. Preë-

pisternal groove strongly impressed below level of scrobe. Basal vein strongly arcuate; first submarginal cell longer than third submarginal cell. Scopa developed on metacoxa, metatrochanter, metafemur, and to varying degrees on metatibia in nonparasitic females; metabasitarusus with distal process and penicillus. Prepygidial fimbria of female distinctly divided by pseudopygidial area.

COMMENTS: Traditionally this subfamily includes three tribes: Augochlorini, Halictini, and Nomioidini; however, see Engel (2000a) for an alternative classification dividing the paraphyletic Halictini into at least five tribes. The classification of Engel (2000a) is adopted here and summarized with slight modification in table 5.

The halictines are the only subfamily of Halictidae recorded from the fossil record. The tribes Caenohalictini (*Eickwortapis*) and Augochlorini (*Augochlora, Neocorynura,* and *Oligochlora*) are present in Miocene amber from the Dominican Republic (table 1). Numerous compression fossils of the Halictini are recorded from the Eocene-Oligocene boundary of Florissant, Colorado (Engel, 1996, unpubl. data), as well as some specimens in scattered, younger deposits throughout the world (e.g., Bachmayer et al., 1971; Engel, 1996; Arillo et al., 1996) but the tribal placement of these fossils is slightly uncertain (all are likely to be Halictini s.s.). Bachofen-Echt (1949) reported a "*Halictus*" from Baltic amber, but I have been unable to locate the material from which he made his determination. Oddly, Bachofen-Echt (1949) referred his fossil "*Halictus*" to the subfamily Apinae (a gross misplacement even allowing for the taxonomic conventions of his time; even the most radical of classifications never classified *Halictus* with the apines!). Below I describe the only definitive halictine in Baltic amber.

TABLE 5
Hierarchical Supragenetic Classification of Halictidae

FAMILY HALICTIDAE THOMSON
Subfamily Rophitinae Schenck
Tribe Rophitini Schenck
Tribe Penapini Engel, new tribe[a]
Subfamily Nomiinae Robertson
Subfamily Halictinae Thomson
Tribe Nomioidini Börner
Tribe Halictini Thomson
Subtribe Halictina Thomson
Subtribe Sphecodina Schenck
Tribe Gastrohalictini Schrottky
Tribe Agapostemonini Engel[b]
Tribe Caenohalictini Michener
Tribe Augochlorini Beebe
Subtribe Corynurina Engel
Subtribe Augochlorina Beebe

[a]Penapini, new tribe (type genus: *Penapis* Michener): Recognized by the combination of elongate, flattened labial palpi; absence of apical lobes on male S7; anterior tentorial pit adjacent outer border of antennal socket; and rectangular subantennal area. Included genera: *Ceblurgus* Urban and Moure, *Goeletapis* Rozen, and *Penapis* Michener. *Xeralictus* is likely near to the Penapini as evidenced by the male terminalia and should perhaps be recognized as its own tribe. Penapini was revised by Rozen (1997).

[b]*Nomen translatum* (elevated from subtribal rank outside of Caenohalictini).

Tribe HALICTINI Thomson

Sphecodidae Schenck, 1869: 316. Type genus: *Sphecodes* Latreille, 1804. Suppressed in favor of Halictina Thomson (Michener, 1991; ICZN, 1993).

Halictina Thomson, 1869: 8. Type genus: *Halictus* Latreille, 1804.

Thrinchostomini Sakagami, 1974: 258. Type genus: *Thrinchostoma* Saussure, 1890.

DIAGNOSIS: This tribe is most similar to the Gastrohalictini (= *Lasioglossum* group) but differs most notably by the strong distal wing venation.

DESCRIPTION: Anterior tentorial pits set in epistomal sulcus (not in clypeus and connected to epistomal sulcus by a distinct sulcus as in Nomioidini); distal wing venation strong; pseudopygidial area of T5 in females lacking a median cleft; *males with a pygidial plate present on the apex of T7*; *males lacking a spiculum*; *first and second metatarsal segments of male not fused.*

COMMENTS: I have used here the narrowed concept of Halictini as presented by Engel (2000a: 67) excluding the weakened wing vein groups, the agapostemonine genera, the caenohalictine genera, and the augochlorine genera. Such a narrowing of the tribe to exclude the latter groups makes the Halictini putatively monophyletic. Table 5 outlines the classification of Halictidae adopted herein.

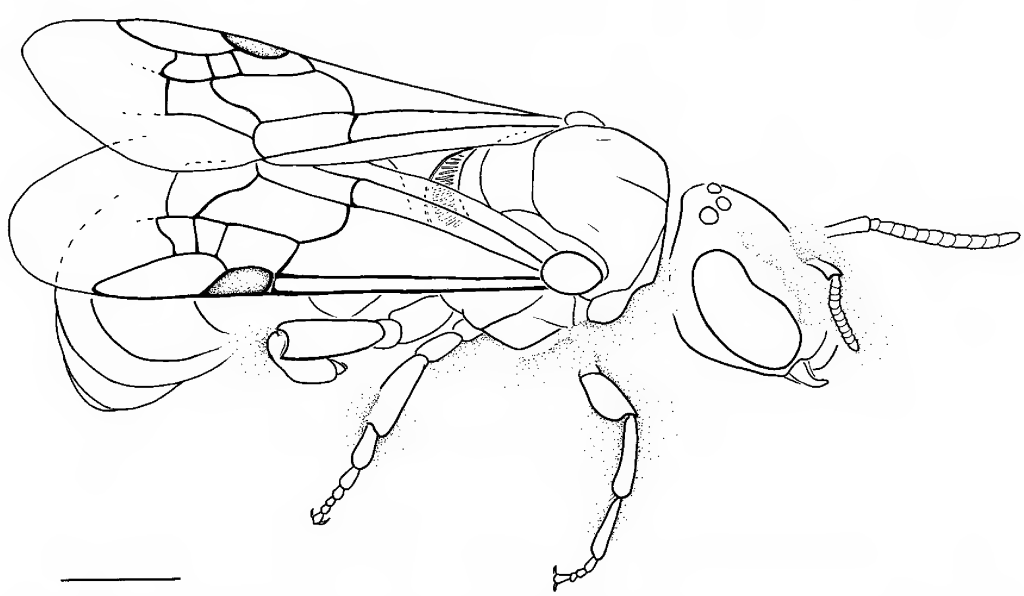


Fig. 8. Right lateral habitus of holotype female of *Electrolictus antiquus,* new species. Scale bar = 1 mm.

***Electrolictus*,** new genus

TYPE SPECIES: *Electrolictus antiquus* Engel, new species.

DIAGNOSIS: This group appears in some respects to be similar to the principally African genus *Patellapis* (sensu Michener, 1978) combining features of the subgenera *Patellapis* s.s. and *Chaetalictus.* From *Chaetalictus* the fossil differs by the strongly bordered metabasitibial plate that is not obsolescent anteriorly, while from *Patellapis* s.s. the fossil differs by the absence of metasomal setal bands. From the whole genus *Patellapis, Electrolictus* can be distinguished by the absence of tomentum, absence of metasomal banding, reception of both m-cu crossveins by the third submarginal cell, and sparse and simple mesosomal pubescence. The reception of both 1m-cu and 2m-cu in the third submarginal cell is reminiscent of *Thrinchostoma* but *Electrolictus* differs from this genus by the absence of tergal setal bands (in *Thrinchostoma* these are formed by laterally directed setae along the apical margins), strong preëpisternal groove, and extremely short malar space. Furthermore, most *Thrinchostoma* (subgenera *Thrinchostoma* s.s. and *Diagonozus*) have a distinctive, dense setal patch near 1rs-m in the forewing which *Electrolictus* lacks.

DESCRIPTION: Mandible with strong subapical tooth, mandible almost bidentate (fig. 11). Malar space much shorter than basal mandibular width, base of mandible nearly touching lower margin of compound eye (fig. 10). Basal area of labrum with a low apical, suborbicular elevation; distal process narrowly triangular and laterally serrate with dense, long, lateral fimbria (fig. 11); distal keel of dorsal process strong without basal expansion, slightly wider at apex. Hypostomal ridge carinate (fig. 11), anterior angle rounded, ridges parallel (not diverging anteriorly). Proboscis not greatly narrowed (length less than six times width); glossa relatively short; maxillary palpal segments about equal in length, total length of palpus about 90% of prementum length. Clypeal truncation without short, lateral processes (fig. 12), lower half of clypeus below lower tangent of compound eyes (fig. 12); clypeus gently convex, not protuberant in lateral view (fig. 10). Epistomal sulcus forming a greatly obtuse angle, nearly linear (fig. 12). Supra-

clypeal area not protuberant in lateral view. F1 about as long F2 (figs. 9, 10). Gena slightly narrower than compound eye in lateral view. Compound eyes without pubescence; inner margins slightly emarginate above level of antennal sockets; eyes slightly converging below. Ocelli not enlarged; interocellar furrow absent (fig. 9). Preoccipital area rounded. Pronotal dorsal ridge carinate; lateral ridge rounded; dorsolateral angle slightly obtuse (fig. 8). Anterior border of mesoscutum broadly rounded (fig. 8), anterior extremity rising well above pronotum but not overhanging, anterior vertical surface curving gently onto dorsal surface; tegula oval; metanotum not tomentose. preëpisternal groove present and strong below level of scrobal groove. Probasitibial comb absent; malus short, slightly shorter than velum, with long, thin pectinate teeth; claws with short inner tooth (fig. 16); arolium present; metabasitibial plate with strong borders, narrowly triangular (fig. 14); inner hind tibial spur pectinate, five long teeth (not including apex) (fig. 15); metabasitarsus with distal process and penicillus. Basal vein strongly arcuate (fig. 13); marginal cell apex feebly truncate and appendiculate; three submarginal cells (fig. 13); both m-cu crossveins entering third submarginal cell (fig. 13); first submarginal cell about as long as combined lengths of second and third submarginal cells; distal wing veins strong. Basal area of propodeum with strong striae radiating to apical margin (fig. 8), not strongly declivitous (nearly horizontal); ridge between basal and posterior surfaces rounded; no carinae on lateral margins of posterior surface. Metasoma with tomentum; T1 broader than long; terga without setal bands (basal or apical); tergal graduli slightly lamellate; metasoma without integumental banding; pseudopygidial area not cleft.

ETYMOLOGY: The new genus-group name is a combination of *electrum* (L. meaning "amber") and *-lictus* (root of the type genus of the Halictini, *Halictus*). The name is masculine.

***Electrolictus antiquus*, new species**

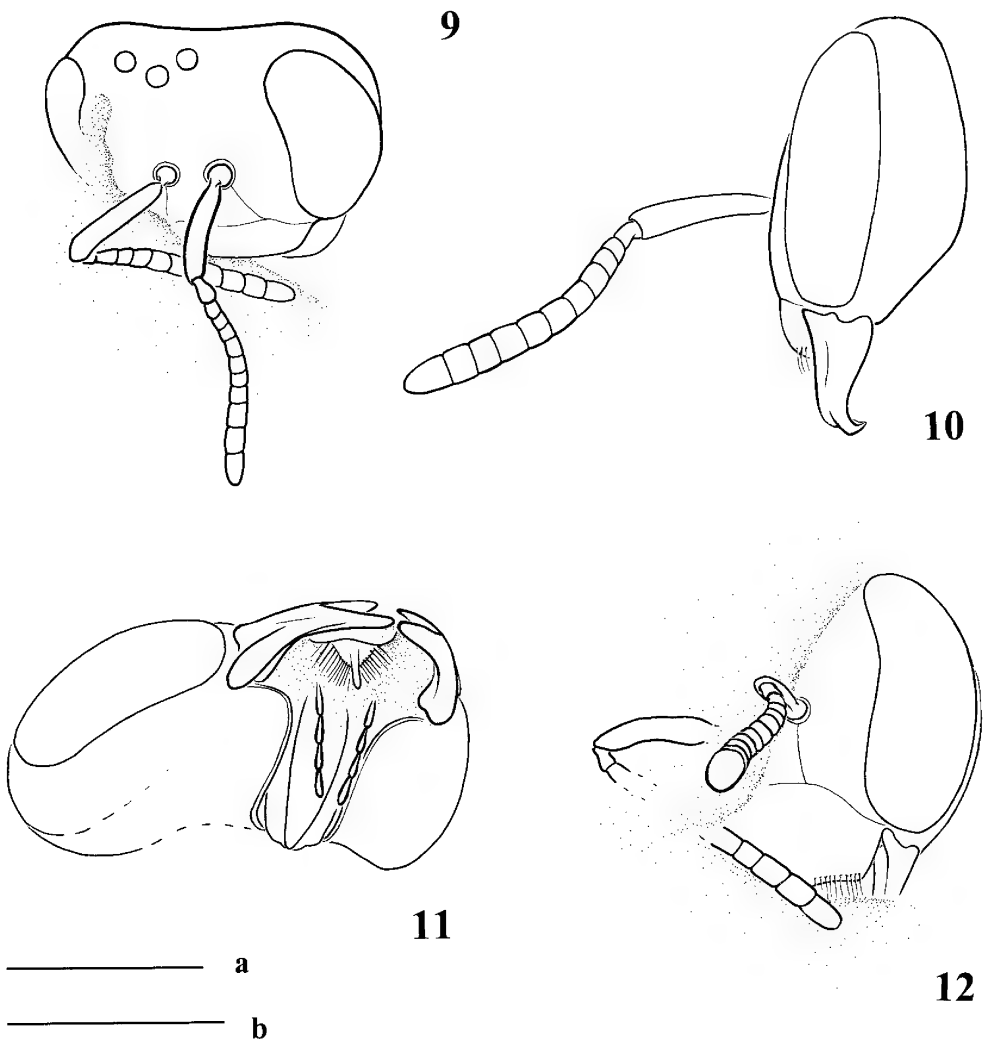
Figures 8–16

Plate 1a,b

DIAGNOSIS: As for the genus.

DESCRIPTION: **Female.** Total body length 8.17 mm; forewing length 5.60 mm. Head slightly longer than wide (length 2.08 mm, width 1.68 mm). Face relatively flat in lateral view. Upper interorbital distance 1.28 mm; lower interorbital distance 1.16 mm. Vertex unmodified, relatively short (ca. 1 OD in length: measured from posterior margin of lateral ocellus to preoccipital area. Interocellar distance 0.36 mm; ocellocular distance 0.28 mm; median ocellus to lateral ocellus 0.12 mm. Median and parapsidal lines relatively strong. Basal vein distad cu-a by about two times vein width; 1m-cu distad 1rs-m by about vein width; 2rs-m distad 2m-cu by about four times vein width, 2rs-m arched (not straight); first submarginal cell about as long as combined lengths of second and third submarginal cells; second submarginal cell slightly narrowed anteriorly; anterior border of second submarginal cell equal to that of third submarginal cell; posterior border of third submarginal cell approximately 1.5 times longer than anterior border.

Clypeus with coarse, faint punctures, punctures separated by a puncture width or less and integument between faintly imbricate on apical third, remainder of clypeus with smaller, well-defined punctures separated by a puncture width or less and integument between smooth. Supraclypeal area sculptured as on upper two-thirds of clypeus. Face with similar punctures as those on supraclypeal area except separated by less than a puncture width, in most places punctures nearly contiguous; integument between punctures smooth; punctures slightly smaller near ocelli. Vertex and gena with minute punctures separated by a puncture width or slightly more, integument between smooth. Postgena faintly imbricate with a few widely scattered coarse punctures. Pronotum smooth; mesoscutum with well-developed punctures separated by 1–2 times a puncture width except around median line punctures slightly more sparse, separated by 2–3 times a puncture width, integument between smooth; tegula smooth except inner margin bordering mesoscutum with minute punctures separated by less than a puncture width; scutellum sculptured as on mesoscutum; metanotum rugulose. Preëpisternum with coarse punctures, punctures nearly contiguous, integument between smooth when evident;



Figs. 9–12. Head of holotype female of *Electrolictus antiquus,* new species. **9.** Dorsofrontal view. **10.** Left lateral view. **11.** Ventral view. **12.** Frontal view. Scale bars = 1 mm (a = figs. 9, 10, 12; b = fig. 11).

mesepisternum sculptured as on preëpisternum except hypoepimeral area with smaller punctures separated by a puncture width or less; metepisternum sculptured as on hypoepimeral area although punctures slightly transversely elongate. Basal area of propodeum with strong striae radiating from basal margin, striae reaching to apical margin of dorsal surface, integument between smooth and shining; lateral surface minutely punctured and faintly imbricate along posterior half. Terga and sterna imbricate.

Head and mesosoma dark brown to black with weak metallic highlights; tegula dark brown. Legs dark brown. Wing membrane hyaline; veins strong and dark brown. Metasoma uniformly dark brown, without integumental banding.

Mandible with moderate length, simple setae scattered along lower margin and on out-

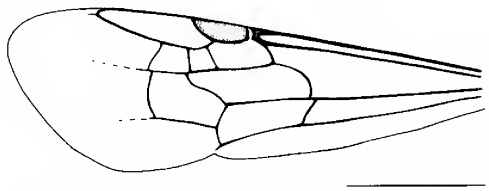


Fig. 13. Forewing of holotype female of *Electrolictus antiquus,* new species. Scale bar = 1 mm.

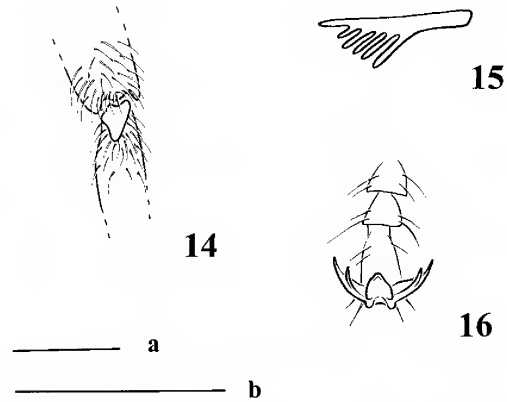
er surface. Clypeus with apical fimbria of simple setae; face, supraclypeal area, and surface of clypeus with short to moderate length, subappressed to suberect, scattered setae each with a few minute branches; setae more sparse on vertex. Gena with subappressed short, scattered setae each with a few minute branches. Postgena with widely scattered, simple setae of moderate length. Mesoscutum with widely scattered, erect, moderate-length setae, each with minute branches; tegula with minute, appressed, simple setae along inner half; scutellum with scattered, long setae, each with numerous minute branches; metanotum with setae as on scutellum. Mesepisternum with scattered, moderate-length, suberect setae, each with several minute branches; metepisternum with sparse, minute, simple, erect setae. Scopa of metafemur with long, plumose setae; similar setae on metatibia although more dense. Lateral and posterior surface of propodeum with sparse, long, simple setae. Terga without tomentum, instead, with sparse, simple, subappressed, short setae; sterna with similar pubescence except setae slightly longer and restricted to apical halves.

MATERIAL: One specimen. **Holotype.** Female, MB.I.1952 (ZMHB): labeled "Holotype, *Electrolictus antiquus* Engel" // "Museum für Naturkunde Berlin, Paläontologisches Museum, Slg. Kühl 23 (3/12), Inv. Nr. MB.I.1952" // "Halictidae: Halictinae, det. M. S. Engel, 1999".

ETYMOLOGY: The specific epithet is the Latin word *antiquus* meaning "ancient" and is a reference to this being the oldest record of an amber halictid.

PALEOMELITTIDAE, New Family

TYPE GENUS: *Paleomelitta* Engel, new genus.



Figs. 14–16. Leg structures of holotype female of *Electrolictus antiquus,* new species. **14.** Metabasitibial plate. **15.** Inner metatibial spur. **16.** Claw, arolium, distitarsus, and apical two segments of mediotarsus. Scale bars = 0.5 mm (a = fig. 14; b = figs. 15, 16).

DIAGNOSIS: This family is a typical short-tongued bee lineage with the cylindrical labial palpus segments and elongate jugal lobe; the latter, plesiomorphic character distinguishing the group from the Melittidae. Paleomelittidae also differs from the melittids by the entirely complete scrobal groove (present only posterior to episternal scrobe and reaching to anterior suture of metepisternum in Melittidae). Unlike the basic short-tongued families, however, Paleomelittidae has a fully exposed mesocoxa.

DESCRIPTION: Single subantennal suture (i.e., subantennal areas absent) meeting inner, lower margin of antennal socket. Facial foveae absent. Segments one and two of labial palpi similar to distal segments, cylindrical, distal segments in line with basal segments; glossa acute, short, without flabellum; stipital concavity and comb absent; galeal comb absent. Preëpisternal groove incomplete, absent below level of scrobe; scrobal groove present and entire (i.e., present both in front of as well as posterior to episternal scrobe). Mesocoxa fully exposed, exposed area slightly longer than distance from summit to metathoracic wing base; metabasibitial plate present; scopa developed on metafemur (more weakly than on following leg segments), metatibia, and metabasitarsus, scopa strongest

on metatibia. Jugal lobe of hind wing much more than half as long as vannal lobe.

COMMENTS: Paleomelittidae occupies an interesting position intermediate between the basic short-tongued families (Colletidae, Halictidae, and Andrenidae) and the "Melittidae + long-tongued families" complex. The family has the fully exposed mesocoxa typical of melittids and long-tongued bees and is therefore closer to this group than to other basic short-tongued families. It could be retained as the basalmost subfamily of Melittidae but this would render the melittids paraphyletic and I have therefore accorded the group family rank.

***Paleomelitta*, new genus**

TYPE SPECIES: *Paleomelitta nigripennis* Engel, new species.

DIAGNOSIS: As for the family (see above). *Paleomelitta* has the general habitus of *Dasypoda* species and the forewing venation of the two genera is somewhat similar in many respects (except in dasypodaines 1m-cu is not strongly apicad the second abscissa of Rs). *Paleomelitta* can be separated from *Dasypoda* by the above familial characters as well as those presented below in the generic description (most notably the absence of a metabasitibial plate in *Dasypoda* is significantly different from *Paleomelitta* where this structure is large and well developed).

DESCRIPTION: As for the family with the following additions: Labrum with two short, medial tubercles on basal surface (fig. 17), about 2.5 times wider than long, without distal process. Mandible broad at base and tapering rapidly to apex, strongly bent inward near midpoint, with strong subapical tooth (fig. 17). Malar space short, much shorter than basal mandibular width. Clypeus slightly concave medially on central disc, apical margin with distinct medial tubercle laterally bordered by tufts of elongate, erect setae (tufts composed of three setae each: fig. 17); epistomal sulcus forming an obtuse angle; apical quarter of clypeus set below lower tangent of compound eyes. Inner margins of compound eyes approximately parallel. F1 longer than F2 (fig. 17); F3 slightly longer than F2. Vertex short, ca. 1.5 OD in length (fig. 18). Posterior margin of scutellum with

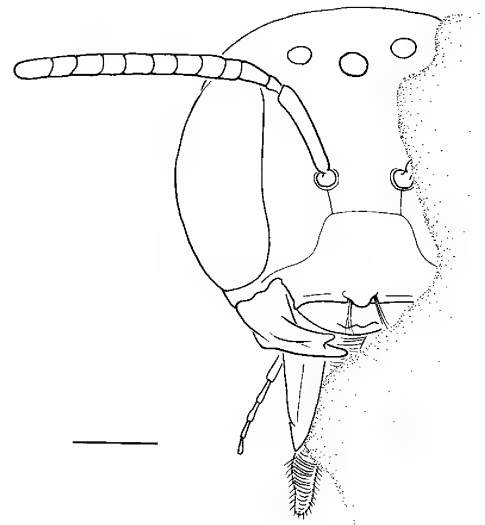


Fig. 17. Frontal view of head of holotype female of *Paleomelitta nigripennis,* new species. Scale bar = 1 mm.

fringe of elongate, simple setae (fig. 18); scutellum rising well above metanotum then abruptly curving behind posterior fringe to meet metanotal basal border, not projecting over metanotum. Metabasitibial plate present, large, and strongly bordered on all edges; scopal setae simple; claws with short inner tooth (fig. 19); arolium present and large (fig. 19). Marginal cell apex set away from wing margin by approximately three-quarters of pterostigma width, feebly appendiculate (fig. 20). Margin of pterostigma inside of marginal cell slightly convex; pterostigma longer than wide; r-rs arising in apical half of pterostigma. Two submarginal cells; second abscissa of Rs approximately orthogonal to M, strongly basad of 1m-cu (fig. 20).

ETYMOLOGY: The new genus-group name is a combination of *palaios* (Greek, meaning "ancient") and *melitta* (Greek, meaning "bee"). The name is feminine.

***Paleomelitta nigripennis*, new species**

Figures 17–20
Plates 1c,d, 2a

DIAGNOSIS: As for the genus.

DESCRIPTION: **Female.** Total body length 14.65 mm; forewing length 10.50 mm. Head

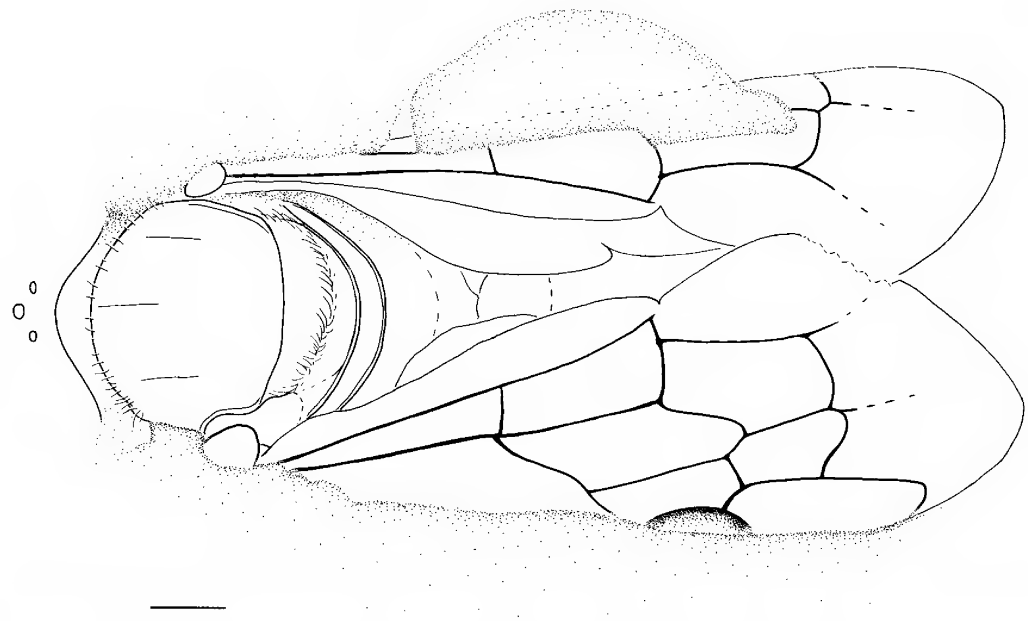


Fig. 18. Dorsal view of mesosoma, posterior border of prosoma, and anterior border of metasoma of holotype female of *Paleomelitta nigripennis,* new species. NOTE: The depicted incision in the hind wing is the jugal fold demarcating the apical margin of the jugal lobe; the vannal fold is positioned just under the posterior edge of the forewing. Scale bar = 1 mm.

wider than long (length 3.25 mm, width 4.03 mm). Compound eye width approximately twice that of gena. Interocellar distance 0.60 mm; ocellocular distance 0.50 mm; median to lateral ocellus 0.15 mm. Median and parapsidal lines strongly impressed (fig. 18). Intertegular distance 3.05 mm; mesoscutum length 1.05 mm; scutellum 2.5 times longer than metanotum; basal area of propodeum about as long as metanotum. Basal vein basad cu-a by vein width; second abscissa of Rs basad 1m-cu by four times vein width, straight, approximately orthogonal to M (fig. 20); 2rs-m distad 2m-cu by two times vein width; first submarginal cell subequal to second submarginal cell; posterior border of second submarginal cell approximately 1.25 times length of anterior border.

Labrum with small punctures separated by a puncture width or less, integument between smooth. Clypeus with small punctures separated by 1–2 times a puncture width on apical half, basal half punctures smaller, faint and sparse, integument between smooth. Supraclypeal area, face, vertex, and gena sculptured as on basal half of clypeus. Pronotum smooth and impunctate. Mesoscutum with small punctures separated by 1–2 times a puncture width except around median line separated by a puncture width or less, integument between smooth. Scutellum sculptured as on mesoscutum except punctures separated by 2–3 times a puncture width. Tegula with minute punctures separated by less than a puncture width on inner half, outer half impunctate, integument between finely imbricate. Metanotum imbricate. Pleura with sparse, minute punctures, integument between smooth. Propodeal lateral and posterior surfaces finely imbricate; basal area of propodeum strongly imbricate. Metasomal terga with minute punctures separated by a puncture width, integument between finely imbricate; sterna imbricate.

Coloration dark brown. Wing membranes exceedingly infumated, dark brown; veins black.

Pubescence fuscous. Labrum with scat-

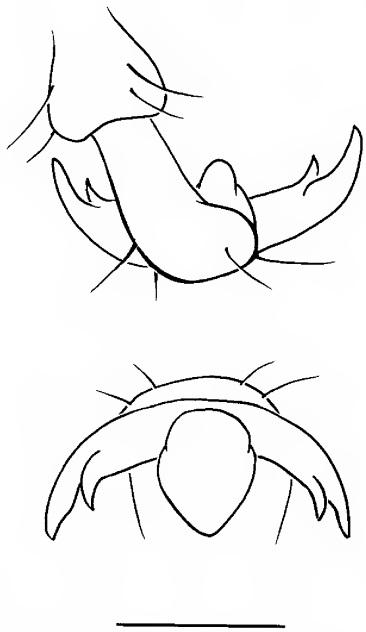


Fig. 19. Distitarsus, claw, and arolium of holotype female of *Paleomelitta nigripennis,* new species. Upper image is an outer view; lower image is an inner view. Scale bar = 0.25 mm.

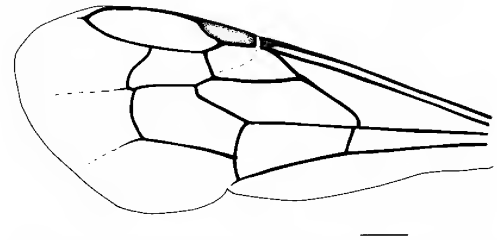


Fig. 20. Forewing of holotype female of *Paleomelitta nigripennis,* new species. Scale bar = 1 mm.

tered, short (ca. 1 OD or less), erect, simple setae. Clypeus and supraclypeal area with scattered, short, suberect, simple setae; clypeus with two submedial patches of three (2 OD in length) simple setae (fig. 17). Face, vertex, and gena with scattered, simple, erect to suberect, short (1 OD in length) setae; setae of gena progressively longer toward postgena (reaching 3 OD in length). Pronotum with sparse, minute, suberect, simple setae except surface at dorsolateral angle and pronotal lobe with dense, plumose setae (1 OD). Mesoscutum with scattered, minute, erect, simple setae, setae sparse on central disc but more noticeable along borders. Scutellar pubescence as described for mesoscutum except posteriorly fringed with dense, plumose setae; axilla with more elongate (1.5–2 OD), simple, erect setae. Metanotum with scattered, short, suberect to erect, simple setae. Pleura with scattered, simple, erect setae (1.5–2 OD) except hypoepimeral area without setae. Lateral and posterior surfaces of propodeum with scattered, short, simple setae; basal area of propodeum without setae. Metafemur without scopal setae; metatibia and metabasitarsus with scopae composed of dense, elongate, simple setae, setae longest on inner surfaces (3–4.5 OD). Anterior-facing surface of T1 with widely spaced, erect setae (2 OD), each with a few minute branches; remaining terga and apical margin of T1 with scattered, minute, simple, appressed setae; sterna with scattered, simple, erect, postgradular setae.

MATERIAL: Two specimens. **Holotype.** Female, B-JH 101 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Paleomelitta nigripennis* Engel". The block of amber containing the two bees is an impressive size (pl. 2a) and measures approximately 13.5 cm in length, 5.5 cm in width, and 3.75 cm in height.

Paratype. Female, in same piece of amber as holotype (see above).

ETYMOLOGY: The specific epithet is a combination of the Latin words *nigra* (meaning "black") and *penna* (meaning "wing") and is a reference to the darkened membrane of the forewings.

Family MELITTIDAE Schenck

Melittidae Schenck, 1860: 136. Type genus: *Melitta* Kirby, 1802.

DIAGNOSIS: This family consists of short-tongued bees with the fully exposed mesocoxa, V-shaped submentum, and short jugal lobe typical of the long-tongued bees while retaining the plesiomorphic "short-tongued" labial structure, absence of a stipital comb and concavity, and absence of a flabellum. Melittids also lack a preëpisternal groove and

the scopa is limited to the metatibia and metabasitarsus.

DESCRIPTION: Labrum frequently much wider than long, apical margin fringed with bristles. Single subantennal suture; suture meets lower margin of antennal socket frequently at midpoint, although sometimes slightly laterad midpoint (either outer or inner side of lower margin), never meeting outer margin of antennal socket. Facial foveae absent. Lower lateral margin of clypeus not bent posteriorly on either side of labrum. Flabellum absent; glossa acute; *glossal rod absent*; paraglossa frequently reduced, sometimes absent; labial palpus with first two segments cylindrical, not sheath-like, third and fourth segments in line with preceding segments, not projecting laterally. *Mentum elongate, tapering basally, curved over submentum to its articulation; apex of mentum articulated with prementum via fragmentum; submentum strongly V-shaped and sclerotized, submental arms articulating with cardines slightly above cardo-stipital articulations.* Galeal blade equal or shorter than stipes, frequently longer than prepalpal section of galea; *galeal comb present*; stipital comb and concavity absent; *basistipital process elongate.* Preëpisternal groove absent. Mesocoxa entirely exposed. Metabasitibial plate frequently distinct. Scopa restricted to metatibia and metabasitarsus. Jugal lobe of hind wing one quarter to one half as long as vannal lobe. Metapostnotum without pubescence. Pygidial plate and fimbria of female present; pygidial plate of male frequently absent. *Volsella present; penis valves do not form a distinct spatha.*

COMMENTS: The subfamily Melittinae (sensu Michener, 1981b) contains three distinct groups that are not closely affiliated; each has numerous characters separating them from one another as much as the remaining subfamilies of the family. Herein I have separated *Macropis* from the subfamily Melittinae and resurrected the subfamily Macropidinae; I have here added a second genus to this subfamily (described below). Likewise, the African genera *Rediviva* and *Redivivoides,* while retained in Melittinae, are restricted to their own tribe. The Melittinae is therefore reduced to two groups: tribe Melittini with *Melitta* s.l. and *Dolichochile,* and tribe **Redivivini** (new tribe; type genus: *Rediviva* Friese) with *Rediviva* and *Redivivoides.* The Redivivini can be separated from Melittini by the reduced, shining, and smooth propodeal triangle and males with S7 bifid (Michener, 1981b). Table 6 summarizes a new higher classification of Melittidae.

TABLE 6
Hierarchical Supraspecific Classification of Melittidae
(Currently recognized genera included but subgenera excluded.)

FAMILY MELITTIDAE SCHENCK
Subfamily Meganomiinae Michener
- Genus *Meganomia* Cockerell
- Genus *Ceratomonia* Michener
- Genus *Uromonia* Michener
- Genus *Pseudophilanthus* Alfken

Subfamily Melittinae Schenck
- Tribe Melittini Schenck
  - Genus *Melitta* Kirby
  - Genus *Dolichochile* Viereck
- Tribe Redivivini Engel
  - Genus *Rediviva* Friese
  - Genus *Redivivoides* Michener

Subfamily Macropidinae Robertson
- †Tribe Eomacropidini Engel
  - †Genus *Eomacropis* Engel
- Tribe Macropidini Robertson
  - Genus *Macropis* Klug

Subfamily Dasypodainae Börner
- Tribe Promelittini Michener
  - Genus *Promelitta* Warncke
- Tribe Dasypodaini Börner
  - Genus *Dasypoda* Latreille
  - Genus *Eremaphanta* Popov
  - Genus *Capicola* Friese
  - Genus *Hesperapis* Cockerell
  - Genus *Xeralictoides* Stage
- Tribe Sambini Michener
  - Genus *Samba* Friese
  - Genus *Haplomelitta* Cockerell

†Extinct.

The separation of *Macropis* from the Melittinae implies that the oil-collecting structures of the Macropidini and the Redivivini arose independently. This seems to be a valid conclusion since macropidines appear to share features with basal dasypodaines (e.g., *Promelitta*) particularly in the presence of only two submarginal cells and, in fact, the structure of the second abscissa Rs in basal

dasypodaines is difficult to distinguish from the state seen in Macropidinae.

Subfamily MACROPIDINAE Robertson

Macropididae Robertson, 1904: 42. Type genus: *Macropis* Panzer, 1809.

DIAGNOSIS: This subfamily resembles the Dasypodainae by the presence of only two submarginal cells in the forewing (i.e., loss of 1rs-m). In dasypodaines, however, the second abscissa of Rs is not widely separated from 1m-cu and is essentially orthogonal to M. From Melittinae, in the restricted sense that I have used it here, macropidines differ by the reduced number of submarginal cells, the presence of yellow maculations on the face of males, and the presence of a pygidial plate in males.

DESCRIPTION: Mandible with strong subapical tooth. Two submarginal cells, cells subequal in length; second abscissa of Rs slightly oblique, widely separated from 1m-cu. Pygidial and prepygidial fimbriae strong. *Males with yellow maculations on the clypeus; males with pygidial plate present.*

COMMENTS: The subfamily as presently defined contains two genera (*Macropis* and *Eomacropis*), which I have segregated into two monobasic tribes. This is owing to the numerous, significant differences between the two genera, each with several apomorphic traits supporting their respective monophyly. They are sufficiently different to warrant placement in different tribes.

EOMACROPIDINI, New Tribe

TYPE GENUS: *Eomacropis* Engel, new genus.

DIAGNOSIS: This tribe differs from Macropidini most notably by the complete absence of the suite of oil-collecting adaptations seen in *Macropis* (e.g., velvety setae on thickened tarsi). Eomacropidini has an elongate metabasitarsus and vein r arises distad the middle of the pterostigma. The apomorphic presence of a strongly convex and medially carinate metanotum and V-shaped propodeum is immediately diagnostic.

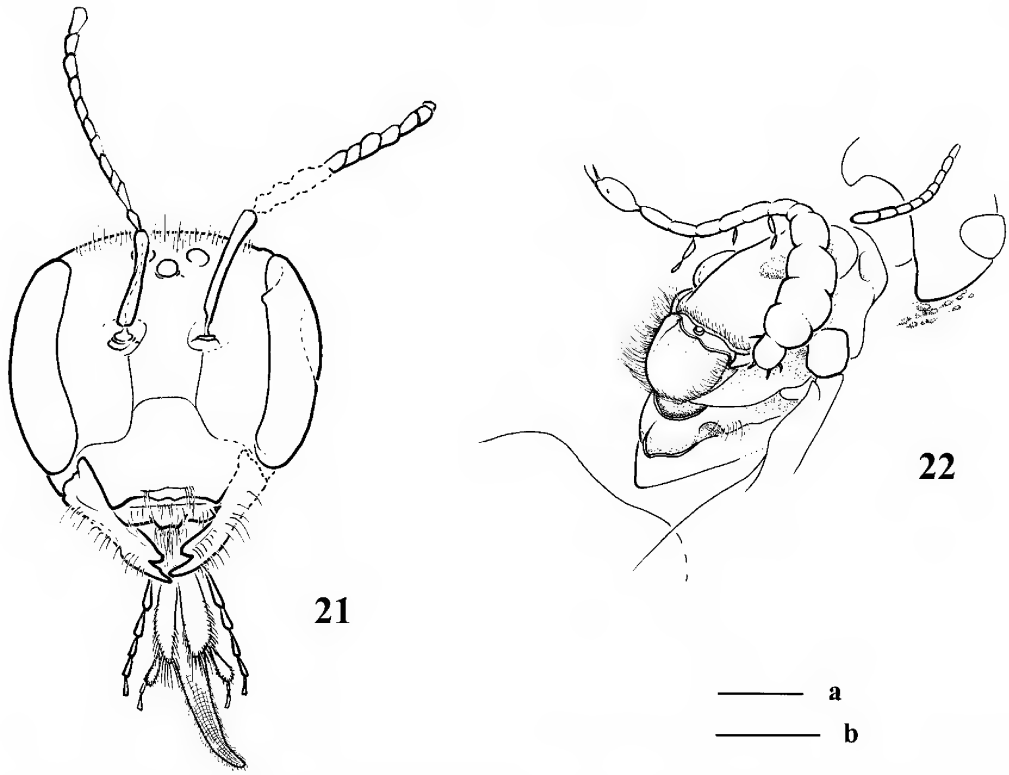
DESCRIPTION: Labrum without median transverse ridge, with subapical elevation (fig. 21). Anterior border of scutellum gently biconcave (straight in Macropidini), posterior border rising well above metanotum (fig. 22) (not gently curving over to meet metanotum as in Macropidini). Metanotum strongly convex, with median longitudinal carina (fig. 22). Protarsi and mesotarsi not thickened, without dense, velvety setae; metatibia and metabasitarsus thin and elongate (not broad as in Macropidini), metabasitarsus at least three times longer than wide (fig. 24); metatibia without oil-collecting setae; metabasitibial plate strong, broadly rounded (fig. 25); metabasitarsus with setae present on distal process; metabasitarsal setae unmodified. Vein r-rs arising distad middle of pterostigma (fig. 23). Propodeum strongly V-shaped, dorsal-facing surface not transverse.

***Eomacropis*,** new genus

TYPE SPECIES: *Eomacropis glaesaria* Engel, new species.

DIAGNOSIS: As for the tribe (see above).

DESCRIPTION: Galea with long setae at apex; maxillary palpus six-segmented (basal segment not visible in figure 21 but is visible from a lateral view of the head). Width of labrum three times greater than length; surface impunctate; short, median, distal process with long setae along margins. Malar space linear, length much less than basal mandibular width, base of mandible nearly touching lower margin of compound eye. Mandible with strong subapical tooth. Epistomal sulcus forming approximately orthogonal angle (fig. 21). F1 longer than F2 (fig. 21). Compound eye weakly emarginate above level of antennal sockets (fig. 21); compound eyes without setae. Gena slightly broader than compound eye in lateral view. Preoccipital area sharply angled but not carinate. Scrobal groove present. Claw with inner tooth, arolium present (fig. 24); metatibial and metabasitarsal scopa composed of densely plumose setae; setae of apical truncation of metabasitarsus not parted to expose narrow strip of integument. Basal vein straight, basad cu-a, basal vein twice as long as first abscissa of Rs (fig. 23); prestigma shorter than margin of pterostigma inside of first submarginal cell, prestigma about as wide as pterostigma; pterostigma inside of marginal cell slightly convex (fig. 23). Basal area of propodeum impunctate, granular and



Figs. 21–22. Holotype female of *Eomacropis glaesaria,* new species. **21.** Frontal view of head. **22.** Right dorsolateral oblique view of mesosoma, posterior border of prosoma, and anterior border of metasoma. NOTE: Staphyliniform beetle larva on mesoscutum of the holotype. Scale bars = 1 mm (a = fig. 22; b = fig. 21).

without pubescence (plesiomorphically similar in this respect to *Macropis* s.s.).

ETYMOLOGY: The new genus-group name is a combination of *eo-* (a reference to the epoch name, Eocene) and *Macropis,* type genus of the Macropidinae. The name is feminine.

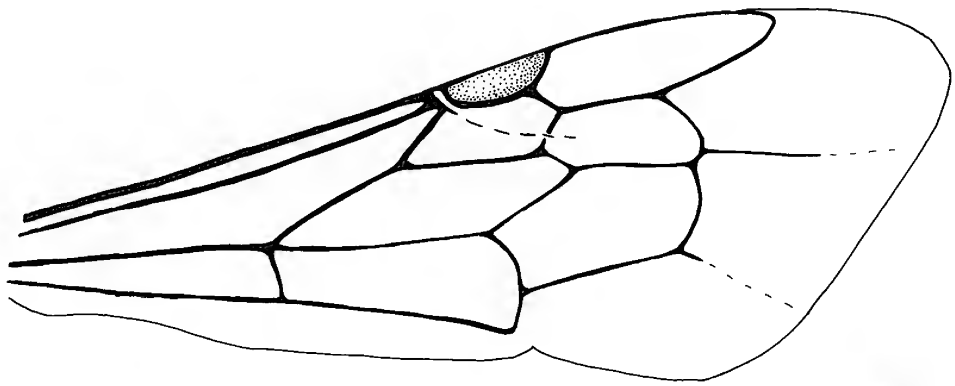
***Eomacropis glaesaria*, new species**

Figures 21–25
Plate 1e,f

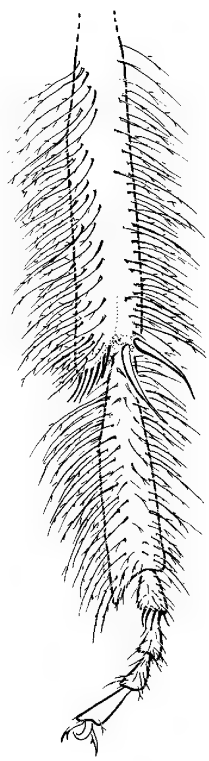
DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 12.4 mm; forewing length 10.1 mm. Head slightly wider than long (length 2.65 mm, width 2.85 mm). Distal half of clypeus extending below lower tangent of compound eyes (fig. 21). Frontal line carinate from antennal sockets to approximately 1 OD from median ocellus. Upper interorbital distance 1.65 mm; lower interorbital distance 1.55 mm. Interocellar distance 0.35 mm; ocellocular distance 0.4 mm; median to lateral ocellus 0.15 mm. Scutellum slightly less than twice length of metanotum; metanotum slightly longer than basal area of propodeum. Malus serrate; distal section of protibial spur beyond velum slightly shorter than section of spur bordering velum. Intertegular distance 1.9 mm. Second abscissa of Rs strongly basad 1m-cu (fig. 23); 2rs-m distad 2m-cu by three times vein width; first submarginal cell slightly shorter than second submarginal cell; eight distal hamuli, arranged in a single evenly spaced series.

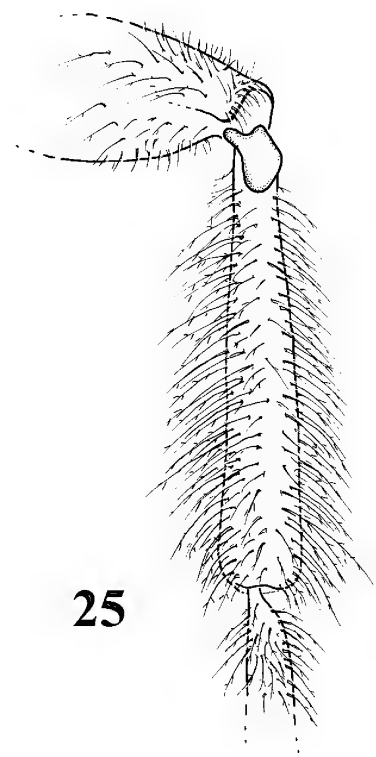
Labrum with minute, scattered punctures,



23



24



25

a

b

integument between smooth. Clypeus with sparse, faint, coarse punctures. Face with small punctures separated by a puncture width, integument between smooth. Vertex with punctures becoming faint, coarse, and sparsely distributed. Gena sculptured like face. Postgena imbricate and impunctate. Mesoscutum and scutellum with small punctures separated by a puncture width or less, integument between smooth. Tegula impunctate and smooth. Metanotum rugulose. Pleura with small punctures separated by a puncture width or less, integument between smooth. Terga and sterna imbricate.

Head dark brown to black with light brown to yellowish marks lateral to clypeus and near lower, inner margin of compound eyes. Mesosoma dark brown to black; legs dark brown. Wing membrane lightly fuscous; veins dark brown. Metasoma dark brown.

Labrum with scattered, short, erect, simple setae. Face with scattered, short, suberect, simple setae. Postgena with moderate-length, erect, simple setae. Mesoscutum with moderate-length, erect, simple seate, a few with minute branches. Scutellum with pubescence as described for mesoscutum except setae longer and with more numerous branches along posterior border. Metanotum with short, scattered setae each with minute branches. Pleura with scattered, long, simple setae, a few with branches, setae becoming progressively longer and more dense ventrally. Scopa on metatibia and metabasitarus composed of dense, long, plumose setae; metafemur with long, branched setae on upper and anterior border. Terga with sparse, minute, simple setae; sterna with scattered, long, simple setae.

MATERIAL: One specimen. **Holotype.** Female (SAMH) labeled: "Holotype, *Eomacropis glaesaria* Engel".

ETYMOLOGY: The specific epithet is derived from the Latin word *glaesarius* (meaning "of amber").

COMMENTS: The holotype of *Eomacropis* is preserved with a staphyliniform beetle larva on its dorsum (fig. 22, pl. 1f). Presumably the two insects were accidentally preserved together, as there is no such association known among living bees today; this, however, does not preclude such an association in the past. Moreover, the beetle is simply too large to have been carried by the bee in the same manner as bees carry triungulin meloids.

LONG-TONGUED BEES

Family MEGACHILIDAE Latreille

DIAGNOSIS: The megachilids are most notable for the development of the scopa on the metasomal sterna [subsequently reduced on the hind legs in Lithurginae (tribe Lithurgini) and Megachilinae; see below] and the structure of the subantennal suture which meets the outer margin of the antennal socket in Lithurginae and Megachilinae. The labrum is broadly articulated to the head capsule and in all except some Fideliinae and the fossils discussed below it is longer than broad.

DESCRIPTION: Labrum broadly articulated to clypeus, frequently longer than wide. Single subantennal suture; suture meets lower margin of antennal socket in Fideliinae, meets outer margin of antennal socket in Megachilinae and Lithurginae. Facial foveae absent. Lower lateral margins of clypeus not bent posteriorly on either side of labrum. Flabellum present; glossa acute; labial palpus with first two segments flattened, sheath-like, and elongate; *submentum strongly V-shaped and sclerotized, submental arms articulating with cardines slightly above cardo-stipital articulations.* Galeal comb absent; stipital comb and concavity present; *basistiptial process elongate.* Preëpisternal groove absent. Mesocoxa entirely exposed. Metabasitibial plate variable (present in Protolithurgini and some Lithurgini along posterior margin; absent in Fideliinae and Megachilinae). Jugal lobe short. Metasomal scopa present (in nonparasitic females). Metapostnotum setose. Pygidial plate and fimbria of female present

←

Figs. 23–25. Holotype female of *Eomacropis glaesaria,* new species. **23.** Forewing. **24.** Inner surface of metatibia and metatarsus. **25.** Outer surface of metatibia, apex of metafemur, and basal portion of metabasitarsus. Scale bars = 1 mm (a = fig. 23; b = figs. 24, 25).

in Fideliinae and Lithurginae, absent in Megachilinae.

COMMENTS: The family Megachilidae consists of three subfamilies: Fideliinae, Lithurginae, and Megachilinae (see table 7). The fideliines have at times been accorded family rank (e.g., Moure and Michener, 1955; Michener and Greenberg, 1980). Within the family the scopa on the hind legs has generally been reduced (owing to the use of the metasomal scopa). It would appear that the scopa of the hind legs has been primitively retained in Fideliinae and an extinct tribe of Lithurginae (Protolithurgini; see below); however, these setae are not used for the transport of pollen (like other megachilids, pollen is transported in the metasomal scopa) and are instead used in flinging sand during nest building (Rozen, 1970, 1973). Thus, these setae in fideliines are not a true scopa.

TABLE 7
Hierarchical Suprageneric Classification of Megachilidae

FAMILY MEGACHILIDAE LATREILLE
Subfamily Fideliinae Cockerell
Tribe Fideliini Cockerell
Tribe Pararhophitini Popov
Subfamily Lithurginae Newman
†Tribe Protolithurgini Engel[a]
Tribe Lithurgini Newman
Subfamily Megachilinae Latreille
Tribe Anthidiini Ashmead
Subtribe Dioxyina Cockerell
Subtribe Anthidiina Ashmead
Tribe Osmiini Newman[b]
†Subtribe Glyptapina Cockerell
†Subtribe Ctenoplectrellina Engel[a]
Subtribe Trypetina Robertson
Subtribe Osmiina Newman
Tribe Megachilini Latreille

†Extinct.

[a]See text for characterization of this new group.

[b]This tribe is admittedly paraphyletic with respect to at least Megachilini. Until such time as a comprehensive worldwide cladistic study of the group has been undertaken I have chosen not to elevate subgroups to tribal rank, something that will eventually be necessary.

Key to Subfamilies of Megachilidae in Baltic Amber

1. Metabasitibial plate present (represented solely along posterior border in living taxa); T1 short and flat in profile; pygidial plate present (sometimes reduced to strong apical spine) ..... Lithurginae Newman
– Metabasitibial plate absent; T1 not shortened, convex in profile; pygidial plate absent ..... Megachilinae Latreille

Subfamily LITHURGINAE Newman

DIAGNOSIS: The Lithurginae can be immediately differentiated by the short, flat first metasomal tergum and the presence of both metabasitibial and pygidial plates. From the Fideliinae it differs by the presence of only two submarginal cells, the reduced seventh sternum in males, and the fusion or loss of volsellae. Megachilines have lost the metabasitibial and pygidial plates and have a longer first metasomal tergum that is convex in profile. Extant lithurgines can further be recognized by their distinctly spiculate tibiae and elongate glossae.

DESCRIPTION: Proboscis elongate, often reaching metasoma in repose (only in the extant tribe Lithurgini); third segment of labial palpus flattened, on same axis as second segment. Labrum longer than broad (except in *Protolithurgus* where the length is apparently equal to the width). Mandibles in recent species with three or more teeth, typically short and robust. Subantennal sutures directed to outer margins of antennal sockets. Outer surfaces of tibiae with hairless spicules (except in *Protolithurgus* and some males of recent species); metabasitibial plate present; metabasitarsus slender and cylindrical (except in *Protolithurgus*). Forewing with two submarginal cells; *jugal lobe of hind wing half or more as long as vannal lobe.* Metasomal T1 shortened, flattened in profile, posterior margin rounded. *Pygidial plate and pygidial fimbria present.* Females typically with a facial prominence below antennal sockets, composed of either clypeus or supraclypeal area (all species of *Microthurge,* nearly all *Lithurgus,* and a few *Trichothurgus*).

COMMENTS: Although classically given subfamilial rank (e.g., Michener, 1944, 1983; Moure, 1949), the group has recently been downgraded to a tribe at the base of the larger subfamily Megachilinae (Michener, 2000a). This has its advantages by emphasizing that lithurgines share more characters in common with the megachilines and that

the difference between the Fideliinae and the remainder of Megachilidae (i.e., Lithurginae and Megachilinae) is great. However, the lithurgines are just as distinctive in their own right, with numerous great differences from the Megachilinae, while differences among the megachiline tribes are far less significant. Thus, since the monophyly of the groups is well established, the recognition of the lithurgines as a separate subfamily seems well warranted and of some use to emphasize their biological and morphological separation from the Megachilinae. Therefore, I here return them to subfamilial rank within the Megachilidae. The subfamily Lithurginae is distributed throughout the world with its greatest diversity in arid regions of South America.

The subfamily has not previously been recorded from any amber deposit and, although one compression fossil has been assigned to *Lithurgus,* definitive lithurgines are not known from the geological record. *Lithurgus adamiticus* (Heer), a compression fossil from the Miocene of Oeningen, was originally proposed as a species of honey bee (Heer, 1865). Cockerell (1909a) later transferred the species to *Lithurgus* on the basis of overall body shape and wing venation. In actuality, the fossil does not preserve characters that would definitively assign it to this subfamily. Thus, the amber inclusion described below is the first definitive fossil lithurgine and serves as both the oldest record of the subfamily and the only one preserved in amber.

A hypothesis of generic relationships within the Lithurginae, Recent and fossil, is presented below (see Cladistic Analyses).

Protolithurgini, New Tribe

Type Genus: *Protolithurgus* Engel, new genus.

Diagnosis: This group can be readily separated from its living sister taxon, the Lithurgini, by the large, strongly bordered metabasitibial plate, the flattened metabasitarsus, the bidentate mandibles, the absence of metatibial spicules, and the relatively short labrum.

Description: Third labial palp segment on same axis as second. Labrum about as long as wide. Mandible bidentate (fig. 26). Outer surfaces of tibiae not spiculate; metabasitibial plate present, strongly bordered on all sides (fig. 28); metatibia with weakly formed scopa in addition to metasomal scopa; metabasitarsus flattened; female claw cleft (fig. 29); female arolium present (fig. 29).

Comments: The Protolithurgini is significant among lithurgines for retaining the plesiomorphic condition of a relatively short glossa, bidentate mandibles, and metatibial scopa (as well as a metasomal scopa). It can be confidently classified in the Lithurginae owing to the apomorphic presence of the shortened and flat first metasomal tergum (unique to lithurgines among the Megachilidae), the third labial palpus on the same axis as the second, and the retention of a metabasitibial plate (although even more well developed than in extant lithurgines).

***Protolithurgus*, new genus**

Type Species: *Protolithurgus ditomeus* Engel, new species.

Diagnosis: Labrum apparently as long as wide, with numerous, erect setae on surface. Mandible not short and stout (as is typical for extant lithurgines), with only two strongly developed teeth (fig. 26). Clypeus not extending below lower tangent of compound eyes (figs. 26, 27); epistomal sulcus forming a slightly obtuse angle; supraclypeal area convex, gently swollen and protuberant in lateral view, extending above level of clypeus (fig. 27). Subantennal sutures meeting outer margin of antennal sockets (fig. 26); F1 distinctly longer than F2 (fig. 26). Compound eyes not emarginate, inner margins parallel (fig. 26). Preoccipital ridge rounded. Tibiae not spiculate; metabasitibial plate present, strongly bordered on all sides, large and broadly rounded (fig. 28); claws cleft (fig. 29); arolium present (fig. 29). Metasomal scopa strong and present; T1 relatively short, flat in lateral view.

Etymology: The new genus-group name is a combination of *protos* (Greek, "first") and the genus name *Lithurgus,* type genus of the subfamily. The name is masculine.

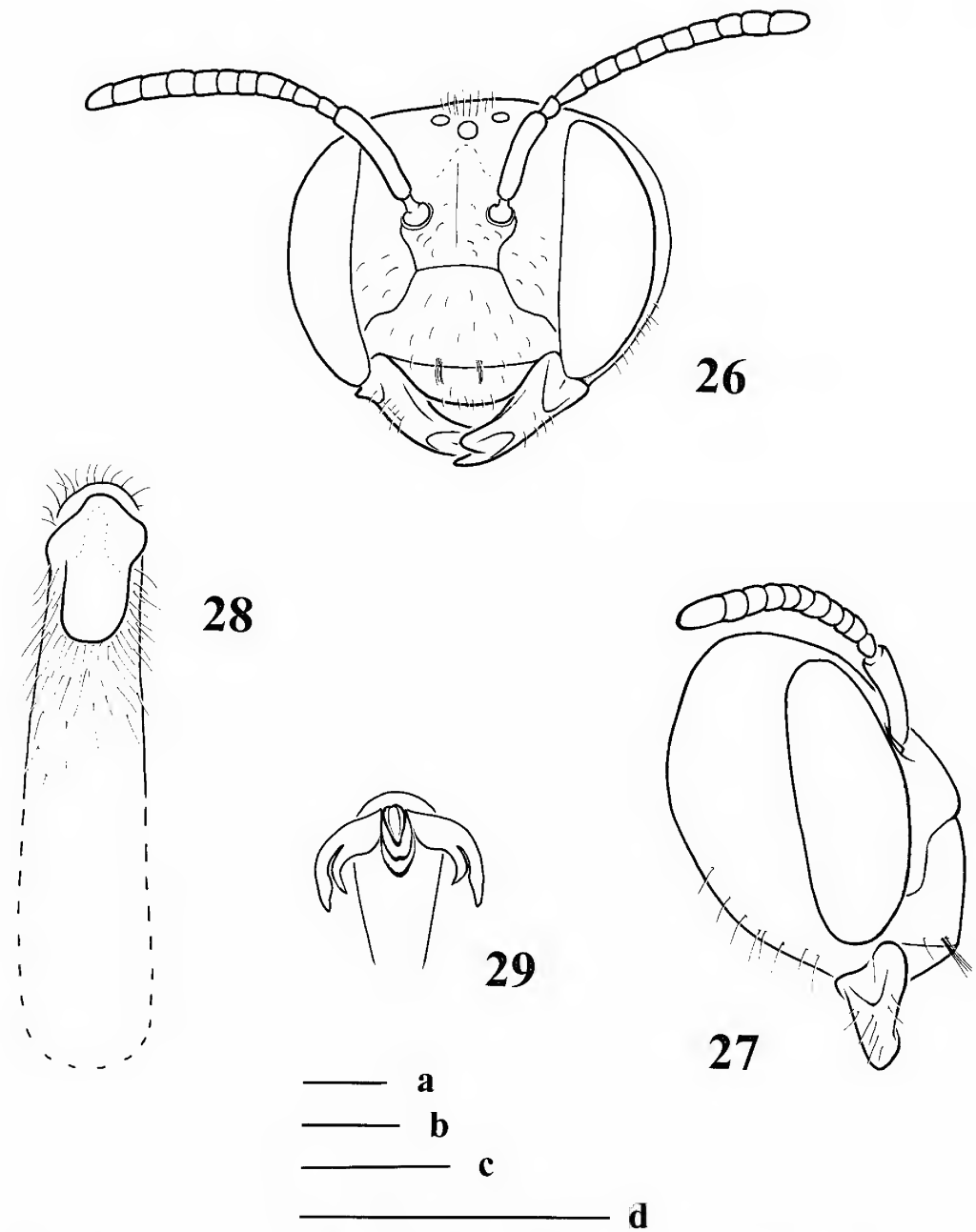
***Protolithurgus ditomeus*, new species**

Figures 26–29

Plate 2b–d

Diagnosis: As for the genus (see above).

Description: **Female.** Preserved body



Figs. 26–29. Holotype female of *Protolithurgus ditomeus,* new species. **26.** Frontal view of head. **27.** Right lateral view of head. **28.** Outer surface of metatibia. **29.** Inner view of claw and arolium. Scale bars = 1 mm (a = fig. 26; b = fig. 27; c = figure 28; d = fig. 29).

length 12.86 mm (from head to approximately the basal portion of T5). Head wider than long (length 3.10 mm, width 4.40 mm). Clypeus not extending below lower tangent of compound eyes; convex and somewhat protuberant in lateral view (fig. 27). Upper interorbital distance 2.35 mm; lower interorbital distance 2.37 mm. Interocellar distance 0.55 mm; ocellocular distance 0.60 mm; median to lateral ocellus 0.15 mm. Intertegular distance 3.38 mm. Scutellum slightly more than three times length of metanotum; metanotum about as long as basal area or propodeum. Basal vein basad by vein width, straight; first submarginal cell apparently subequal in length to second submarginal cell.

Labrum, clypeus, supraclypeal area, face, vertex, gena, and postgena imbricate. Mesosoma imbricate. Metasoma apparently (where evident) imbricate.

Head and mesosoma brown with nonmetallic, greenish highlights; antennae, metasoma, and legs dark brown without highlights. Wing membrane fuscous; veins dark brown to black.

Pubescence fuscous to black. Labrum with numerous, long (2–2.5 OD), simple, erect setae, setae not obscuring integument. Clypeus, supraclypeal area, and face below level of antennal sockets with scattered, simple, erect, long (2–3 OD) setae; clypeal margin with submedial patch of setae; face above level of antennal sockets, vertex, and gena with setae sparser and shorter (1 OD). Postgena with long (2–3.5 OD), erect, simple setae. Pronotum with minute, sparse, simple setae except dorsolateral angle with plumose (1 OD) setae. Mesoscutum with minute, sparse, simple setae. Scutellum as described for mesoscutum except axilla with patches of erect, plumose (1 OD) setae. Metanotum without setae. Hypoepimeral area, metepisternum, and lateral surface of propodeum with sparse, suberect, simple (1 OD) setae; preëpisternum and mesepisternum with scattered, long (2.5–3 OD), erect setae each with a few short branches. Basal area of propodeum without pubescence. Metafemur without scopal setae; metatibia and metabasitarsus with dense, simple setae, a few with two or three short branches. Metasomal terga apparently (where evident) with sparse, minute, simple setae; metasomal sterna with scopa, sterna with dense, elongate (4–5.5 OD), simple, erect setae, setae with sinuous apices.

MATERIAL: One specimen. **Holotype.** Female, B-W 157 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Protolithurgus ditomeus* Engel". The caudal end of the holotype of *Protolithurgus* is badly damaged. The apex of the wings and metasoma reach to the amber surface where the amber becomes extremely turbulent (numerous, strong, bending flow lines). The apices of the wings are missing as is, apparently, the apex of the metasoma. The apical halves of the forewings appear as though they have been cleared and even heated during preservation (while the resin was still soft). Although the veins are no longer pigmented the membrane of the wing is still preserved (the minute setae of the wing membrane can be easily seen at higher magnification) and by slowly searching the wing membrane it is possible to locate the remnants of veins and to follow their courses. Thus, it is possible to determine to some degree what the forewing venation of this species had been. It is also difficult to examine T1 but its apical margin can be seen from above and between the bases of the forewings (which are folded over the metasoma) as well as in lateral view.

ETYMOLOGY: The specific epithet is a reference to the two teeth of the mandible by comparison to the three teeth of Recent lithurgines (Gr. *di,* meaning "two", and *tomeus,* meaning "tooth").

COMMENTS: The holotype of *Protolithurgus ditomeus* has at least eight triungulin meloids hanging onto seta of the mesosomal venter as well as one attached to a seta of the gena. Although a triungulin is recorded by Larsson (1978) in Baltic amber, the specimen was found in isolation from any other insects and its identity was suspect. The triungula reported here are presently the oldest, definitive record of the host-parasite association between bees and meloid beetles as well as the oldest, definitive fossil of a meloid triungulin.

Subfamily MEGACHILINAE Latreille

Megachiles Latreille, 1802b: 381. Type genus: *Megachile* Latreille, 1802a.

DIAGNOSIS: Refer to Diagnosis for subfamily Lithurginae (above).

DESCRIPTION: Proboscis typically not elongate (as in Recent lithurgines); third segment of labial palpus projecting laterally from axis of second segment (except in some *Chelostoma* and other groups). Labrum longer than broad (except in Glyptapina and Ctenoplectrellina). Mandibles with a variable number of teeth, typically short and robust. Subantennal sutures directed to outer margin of antennal sockets. Outer surface of tibiae frequently not spiculate (except in some Anthidiini); metabasitibial plate absent; metabasitarsus flattened. Forewing with two submarginal cells (i.e., 1rs-m absent); jugal lobe of hind wing short. Metasomal T1 not shortened, convex in profile, posterior margin straight or convex. Pygidial plate and pygidial fimbria absent.

Tribe OSMIINI Newman

Osmiites Newman, 1834: 401. Type genus: *Osmia* Panzer, 1806.

Chelostomidae Kirby, 1837: 270. Type genus: *Chelostoma* Latreille, 1809.

Glyptapinae Cockerell, 1909b: 13. Type genus: *Glyptapis* Cockerell, 1909a. NEW SYNONYMY.

Trypetini Robertson, 1903: 164. Type genus: *Trypetes* Schenck, 1861.

Heriadini Michener, 1941: 152. Type genus: *Heriades* Spinola, 1808.

DIAGNOSIS: Megachiline bees with an arolium, an elongate pterostigma, 2m-cu basad 2rs-m, and frequently with simple claws (except in the Baltic amber genera and one living group).

DESCRIPTION: Arolium present; claws simple (except cleft in Glyptapina, Ctenoplectrellina, and *Metallinella*). Pterostigma longer than wide; 2m-cu basad 2rs-m. Integument without maculations (except in *Ochreriades*) and frequently metallic or with metallic highlights.

COMMENTS: Phylogenetic affinities among osmiine genera are unclear and difficult to resolve. The tribe is very likely paraphyletic with respect to at least the Megachilini. Michener (1941) attempted to divide the group into two tribes, the Osmiini s.s. and the Heriadini [roughly equivalent to the *Osmia*- and *Heriades*-genus groups of Griswold (1985), Griswold and Michener (1997), and Michener (2000a)]. Although these groups are not presently well defined, I prefer to tentatively recognize them as subtribes for purposes of comparison with the plesiomorphic fossils discussed below. The Osmiini can therefore be divided into four groups or subtribes as indicated in table 7; the fossils fall into two distinct subtribes: Glyptapina Cockerell and Ctenoplectrellina (**new subtribe**). The two fossil subtribes retain a short labrum, a plesiomorphic feature for Lithurginae and Megachilinae; however, the presence of several derived characters typical of Megachilinae (e.g., complete absence of metabasitibial plate, absence of pygidial plate) suggests that this character is a reversal. Subtribes of Osmiini can be distinguished as follows (based on females only):

Osmiina Newman: Maxillary palpi four- or five-segmented; labrum longer than wide; mandible variously structured; parapsidal lines punctiform (in *Osmia*) or linear; omaular ridge rounded; basal area of propodeum declivitous; claws simple (except in *Metalinella*).

Trypetina Robertson, *nomen translatum* [= Heriadini of Michener (1941)]: Maxillary palpi two- to four-segmented; labrum longer than wide; mandible variously structured; parapsidal lines linear; omaular ridge usually rounded (carinate in some); basal area of propodeum usually horizontal; claws simple. The family-group name based on *Trypetes* (a junior synonym of *Heriades*) has priority over that based on *Heriades.* The name Trypetini cannot be dismissed simply owing to the synonymy of its type genus (ICZN, 1999b: Art. 40.1) and, thus, the subtribal name should be Trypetina Robertson.

Glyptapina Cockerell, *nomen translatum* (includes only *Glyptapis* Cockerell): Maxillary palpi four-segmented; labrum wider than long; mandible with long, upper cutting-edge (figs. 30, 32) (mandible in general structure similar to some species of Anthidiini; e.g., some *Dianthidium*); parapsidal lines linear; omaular ridge strongly carinate (as in some Old World Anthidiini); basal area of propodeum declivitous; claws cleft (fig. 35).

Ctenoplectrellina, new subtribe (type genus: *Ctenoplectrella* Cockerell; subtribe also includes *Glaesosmia,* n. gen.): Maxillary palpi four-segmented; labrum wider than long; mandible variously structured; parapsidal

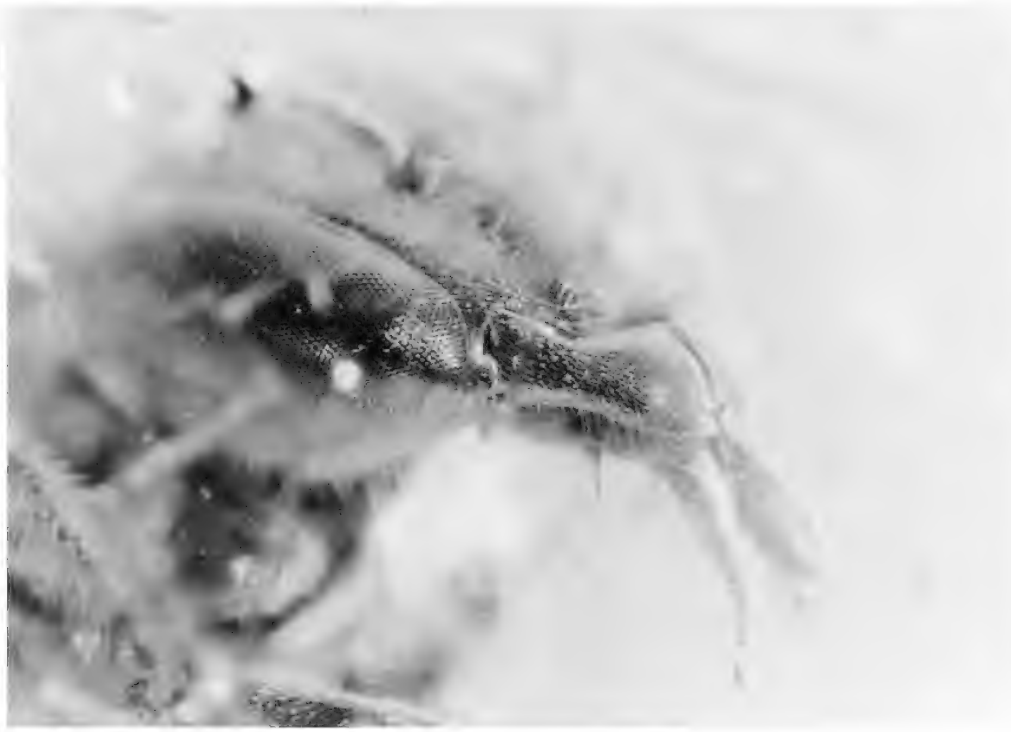


Fig. 30. Right lateral view of head of holotype female of *Glyptapis mirabilis* Cockerell.

lines linear; omaular ridge rounded; basal area of propodeum gently sloping, not strongly declivitous (fig. 46); claws cleft (fig. 42).

It may be that Osmiini, incorporating the fossil lineages, is paraphyletic with respect to not only the Megachilini but the Anthidiini as well. It is possible that Cockerell's Glyptapina (Cockerell, 1909b: Glyptapinae in his system) is more closely allied to Anthidiini, while Ctenoplectrellina is sister to living Osmiini + Megachilini. Once the classification of Osmiini has been clarified through a detailed cladistic study, the fossil groups will likely need to be elevated to tribal status (as will other generic groups of Osmiini).

Key to Genera of Osmiini in Baltic Amber

1. Mesepisternum punctate, not areolate; omaular carina absent, omaulus rounded; propodeum imbricate or smooth, without areolae; mandible with three teeth, short cutting edge between uppermost tooth and lower two teeth (fig. 40); mesoscutum and scutellum normally punctate or impunctate; compound eyes bare (fig. 40) 2
– Mesepisternum coarsely areolate and rugose (figs. 33, 39); omaular carina present and strong (fig. 33); propodeum strongly areolate (fig. 31); mandible with a single, small lower tooth and large upper cutting edge (fig. 32); mesoscutum and scutellum coarsely punctate, punctures deep and craterlike (figs. 31, 38); compound eyes hirsute, setae long (fig. 32) . . . . . *Glyptapis* Cockerell
2. Upper gena much narrower than compound eye in lateral view; subantennal sutures longer than diameter of antennal sockets (fig. 40); distance between compound eyes equal to or slightly less than length of compound eyes; second abscissa Rs orthogonal to vein M (figs. 41, 43) . . . . . *Ctenoplectrella* Cockerell
– Upper gena as broad as compound eye in lateral view; subantennal sutures as long as diameter of antennal sockets; distance be-

tween compound eyes greater than length of compound eyes; second abscissa of Rs angulate such that angle between this vein and M opening toward wing apex is acute (fig. 47) . . . . . *Glaesosmia,* n. gen.

Genus *Glyptapis* Cockerell

Glyptapis Cockerell, 1909a: 314. Type species: *Glyptapis mirabilis* Cockerell, 1909a, monobasic [also designated by Cockerell, 1909b]. Cockerell, 1909b: 13.

DIAGNOSIS: This genus can be instantly recognized by the strong areolate sculpturing of the pleura and propodeum as well as the strong and large punctures of the mesoscutum and scutellum. Furthermore, the long cutting edge of the mandible with a single, sharp, lower tooth and the hirsute compound eyes serve to distinguish *Glyptapis* species from not only Baltic amber megachilids but from all other Baltic amber bees. *Glyptapis* can be separated from other genera, living and extinct, placed in the paraphyletic Osmiini by the characters presented above for the subtribe Glyptapina.

DESCRIPTION: Mandible with a single, small, sharp tooth on lower apical margin and large upper cutting edge (the mandible is similar in general structure to that of some anthidiines) (figs. 30, 32, 33). Malar space short, much shorter than basal mandibular width. Clypeus flat; extending just below lower tangent of compound eyes (fig. 32). Hypostomal ridge carinate, anterior angle rounded. Compound eyes hirsute, setae long (much longer than thrice ommatidial diameter) (fig. 32); compound eye broader than gena in lateral view; inner margins straight and slightly converging below. F1 longer than F2; length of F2 approximately equal to that of F3. Posterior margin of vertex gently concave. Preoccipital area sharply angled and weakly carinate. Mesoscutum and scutellum coarsely and deeply punctate (figs. 31, 38), mesoscutal anterior border broadly rounded; median line moderately impressed; parapsidal lines faintly impressed and linear (not punctiform); tegula oval; scutellum low, weakly convex, not overhanging metanotum, anterior margin with distinct, small, median V-shaped notch, smaller lateral notches present along anterior margin where scutellum laterally bends toward mesoscutum; metanotum slightly inclined but generally not far off from horizontal; mesepisternum strongly areolate, with precoxal triangle along anterior border of mesocoxa; scrobal suture absent; anterior and posterior borders of metepisternum converging ventrally and meeting one another at point of mesocoxal base; propodeum strongly areolate. Claws with strong inner tooth, inner tooth shorter than outer; arolium present (fig. 35); outer apex of mesotibia with a very short, broad, apical spine, similar spine on protibial apex, although much shorter than that of mesotibia; two metatibial spurs, spurs minutely ciliate; metatiba with scattered, elongate, simple setae (fig. 36). Basal vein strongly arcuate (fig. 37). No apparent maculations on integument (coloration is, however, not well preserved in any of the known specimens).

COMMENTS: I had earlier not considered *Glyptapis* to be a megachilid (Engel, 1999d); however, having now seen type material of this genus in the Institut und Museum für Geologie und Paläontologie, I recognize that this genus is, in fact, quite clearly an enigmatic lineage of megachilines (as is the genus *Ctenoplectrella*; see below). The presence of a single subantennal suture that meets the antennal sockets at their outer margin is known only in Megachilidae and the absence of basitibial and pygidial plates as well as possession of only two submarginal cells is indicative of Megachilinae. Although the coarse sculpturing on the pleura is somewhat suggestive of some Old World Anthidiini, as is the presence of a strong omaular carina, the apparent absence of integumental markings, the basal position of 1m-cu relative to the second abscissa of Rs, and the relatively long pterostigma excludes *Glyptapis* from that tribe (see also Comments above under Osmiini). The subtribe Glyptapina (defined above) may eventually prove to represent a lineage more closely allied to the anthidiines (or from which the anthidiines arose: i.e., glyptapines may be stem-group anthidiines), in which case tribal status for this fossil group would be warranted owing to its numerous, plesiomorphic osmiine features, not too mention its own peculiar apomorphies (i.e., sculpturing of mesosoma, elongate eye setae).

Key to Species of *GLYPTAPIS*

1. Mesoscutum with punctures approximately one-third ocellar diameter or less and well spaced (not nearly contiguous) (fig. 38); precoxal triangle bordered anteriorly by narrow, glabrous margin many times less than width of areolae 2
– Mesoscutum with punctures large, approximately one-half ocellar diameter, and nearly contiguous (fig. 31); precoxal triangle bordered anteriorly by wide glabrous margin at least 1.5 times width of areolae . . . . . *G. mirabilis* Cockerell
2. Precoxal triangle containing distinct transverse ridges or striae to form a single, dorsoventral row of areolae 3
– Precoxal triangle without areolae (fig. 33) . . . . . *G. disareolata,* n. sp.
3. Deep, crater-like punctures of scutellum not restricted to posterior two-thirds; metanotum with minute punctures separated by 2–3 times puncture width. . . . . *G. fuscula* Cockerell
– Deep, crater-like punctures of scutellum restricted to posterior two-thirds; metanotum with small punctures densely packed, separated by puncture width or less . . . . . *G. densopunctata,* n. sp.

Glyptapis mirabilis Cockerell

Figures 30, 31

Frontispiece and Plate 2e

Glyptapis mirabilis Cockerell, 1909a: 314.

DIAGNOSIS: This species can be separated from all other *Glyptapis* by the large and nearly contiguous punctures of the mesoscutum. Additionally, the precoxal triangle is well separated from the areolate sculpturing of the remainder of the mesepisternum; the width of the glabrous margin demarcating the anterior border of the precoxal triangle is more than the diameter of the areolae (approximately 1.5 times areolae diameter in width).

DESCRIPTION: **Female.** Total body length 5.92 mm; forewing length 4.04 mm. Head slightly wider than long (length 1.48 mm, width 1.56 mm). Upper interorbital distance 1.08 mm; lower interorbital distance 0.72 mm. Interocellar distance 0.36 mm; ocellocular distance 0.28 mm; median to lateral ocellus 0.12 mm. Intertegular distance 1.48 mm. Basal vein strongly arcuate, confluent with cu-a; first submarginal cell longer than second. 1m-cu enters second submarginal cell about four times vein width distad of second abscissa of Rs; 2rs-m distad 2m-cu by two times vein width; second submarginal cell gently narrowed anteriorly; 2rs-m gently curved; cu-a long; inner margin of pterostigma in first submarginal cell longer than width of pterostigma; inner margin of pterostigma in marginal cell gently convex; marginal cell apex acutely rounded, offset from wing margin by width of vein, not appendiculate. Six distal hamuli arranged in a single, evenly spaced series.

Integument generally shining. Mandible smooth and shining, without outer grooves, with faint, small punctures separated by less than a puncture width on basal half. Clypeus with small, faint punctures separated by 1–2 times puncture width, such punctures particularly faint on apical third, integument between punctures smooth. Supraclypeal area sculptured as on clypeus. Face with minute punctures, more well-defined than those of clypeus and supraclypeal area, punctures separated by 1–2 times puncture width, integument between punctures smooth; punctures becoming faint on vertex. Gena with minute, faint punctures separated by 2–3 times puncture width, integument between punctures smooth. Postgena smooth and impunctate. Pronotum with very sparse, minute punctures, also with minute, transverse striae running along posterior edge of lateral ridge, integument otherwise smooth. Mesoscutum strongly punctured; punctures large (ca. 0.5 OD) and deep, separated by less than one-half a puncture diameter (i.e., nearly contiguous), integument between such punctures smooth, with minute punctures separated (where apparent) by three or more times their own diameter (fig. 31). Tegula with minute punctures separated by two times puncture width, integument between smooth. Scutellum sculptured as on mesoscutum. Metanotum with large lateral pits, medially with minute punctures separated by 2–3 times puncture width, integument otherwise smooth. Preëpisternal area (here used for anterior-facing surface of mesepisternum anterior to omaular carina: preepisternal suture is absent, as in other long-tongued bees) smooth and impunctate. Mesepisternum coarsely reticulate-areolate, integument inside areolae

Fig. 31. Dorsal view of mesosoma of holotype female of *Glyptapis mirabilis* Cockerell.

smooth; scrobal suture absent (perhaps utterly obscured by coarse areolate sculpturing?); precoxal triangle with eight dorsoventral areolae (the number of areolae, however, are variable; in one other specimen there are only four areolae); precoxal triangle anteriorly separated from remainder of mesepisternum by broad glabrous margin that is approximately 1.5 times areola diameter in width. Metepisternum transversely striate, integument between striae smooth. Basal area of propodeum strongly areolate, areolae easily 1 OD in diameter, basal area two areolae in length and eight areolae wide, lateral areolae more rectangular than square areolae near midline; metapostnotum smooth and impunctate, bordered by areolae (0.5 OD in diameter) that converge ventrally just below propodeal pit; outside of areolate borders of metapostnotum on posterior propodeal surface a small glabrous zone of about 1 OD in width; lateral and ventral borders of posterior surface strongly areolate; lateral surface of propodeum dorsoventrally striate, integument between striae smooth. Metasomal terga and sterna faintly imbricate and impunctate.

Color not well preserved, apparently entirely dark brown without maculations. Wing membrane hyaline; veins strong and dark brown.

Mandible with minute, simple, subappressed setae, longer on ventral border. Galea with long setae at apex and on inner border near apex. Clypeus with minute, appressed, simple setae not obscuring integument, such setae also on face below level of antennal sockets. Widely scattered, longer, erect setae on face, clypeus, supraclypeal area; appressed, minute setae disappearing by supraclypeal area, replaced on upper face by aforementioned longer, erect setae, although now more numerous, such setae long on vertex and each bearing a few minute branches. Gena with similar setae as those of vertex, although shorter, subappressed (not obscuring integument), and simple. Postgena with long, erect, widely scattered setae. Pronotum with scattered, minute, simple setae, appressed but not obscuring the integument except on pronotal lobe where setae appear dense and short and along dorsal carina, with setae short, erect, and each with a few minute branches. Mesoscutum with short, plumose setae arising out of large, deep punctures, also with minute, sparse setae in interspaces between punctures. Tegula with minute, appressed, simple setae not obscuring integument. Scutellum with pubescence as on mesoscutum except setae slightly longer. Metanotum with minute, erect, simple setae widely scattered. Preëpisternal area without pubescence; setae of mesepisternum (posterior to omaular carina) as on mesoscutum; metepisternum with scattered, short, simple setae. Basal area and posterior surface of propodeum without pubescence; lateral surface of propodeum with pubescence as described for metepisternum. Pubescence of legs generally simple and short except those setae of tarsi long; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with numerous, somewhat long, setae on all surfaces, most of those on inner surface simple but a few with minute branches, those of outer surface with several short branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sterna as for terga except along apical thirds setae longer, erect, simple, and more numerous (to form metasomal scopa).

MATERIAL: Three specimens. **Holotype.** Female, K72 (IMGP) labeled: "K72, *Glyptapis mirabilis* n. sp., Geologisch-Paläontologisches Institut und Museum, Göttingen" // "Holotype, *Glyptapis mirabilis* Cockerell".

Non-type. Female (CMSE) labeled: "*Glyptapis mirabilis*? Cockerell, det. M. S. Engel".

Non-type. Female, Nr. 33–00524 (CGHG) labeled: "Nr. 33–00524" // "*Glyptapis mirabilis* Cockerell, det. M. S. Engel".

***Glyptapis disareolata*, new species**

Figures 32–35
Plate 2f

DIAGNOSIS: This species is most similar to *G. fuscula* but differs most notably by the absence of areolae in the precoxal triangle.

DESCRIPTION: **Female.** Total body length 5.84 mm; forewing length 4.25 mm. Head

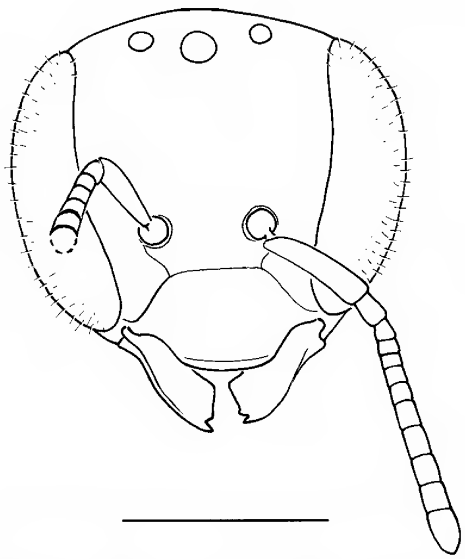


Fig. 32. Frontal view of head of holotype female of *Glyptapis disareolata,* new species. Scale bar = 1 mm.

slightly wider than long (length 1.63 mm, width 1.91 mm). Upper interorbital distance 1.22 mm; lower interorbital distance 0.94 mm. Interocellar distance 0.38 mm; ocellocular distance 0.28 mm; median to lateral ocellus 0.16 mm. Intertegular distance 1.47 mm. Basal vein confluent with cu-a; first submarginal cell longer than second; 1m-cu enters second submarginal cell about four times vein width distad of second abscissa of Rs; 2rs-m distad 2m-cu by two times vein width; second submarginal cell gently narrowed anteriorly; 2rs-m gently curved; cu-a long; inner margin of pterostigma in first submarginal cell longer than width of pterostigma; inner margin of pterostigma in marginal cell gently convex; marginal cell apex acutely rounded, offset from wing margin by width of vein, not appendiculate; six distal hamuli, arranged in a single evenly spaced series (fig. 34).

Integument generally shining. Mandible with minute punctures separated by 1–2 times a puncture width, integument between smooth. Clypeus with minute punctures separated by 1–2 times puncture width, integument between smooth. Supraclypeal area sculptured as on clypeus. Face and vertex with minute punctures, more well-defined than those of clypeus and supraclypeal area, punctures separated by a puncture width, integument between smooth. Gena and postgena with minute punctures separated by a puncture width, integument between smooth. Pronotum with minute punctures separated by a puncture width, also with minute, transverse striae running along posterior edge of lateral ridge, integument between smooth. Mesoscutum strongly punctured; punctures moderately large (ca. 1/3 OD) and deep, separated by less 0.5–2 times puncture width, integument between such punctures smooth with minute punctures separated by 1–2 times their own diameter; anterior border of mesoscutum with deeper puncture closely packed. Tegula with minute punctures separated by a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum except deep punctures restricted to posterior two-thirds. Metanotum with minute punctures separated by a puncture width, integument between smooth. Preëpisternal area (here used for anterior-facing surface of mesepisternum anterior to omaular carina: preepisternal suture is absent, as in other long-tongued bees) with minute punctures separated by a puncture width, integument between smooth. Mesepisternum coarsely reticulate-areolate, integument inside areolae smooth; precoxal triangle anteriorly separated from remainder of mesepisternum by narrow glabrous margin that is less than 0.5 times areola diameter in width, precoxal triangle without areolae (fig. 33). Metepisternum transversely striate, integument between striae smooth. Basal area of propodeum strongly areolate, areolae easily 1 OD in diameter, basal area two areolae in length and eight areolae wide; metapostnotum smooth and impunctate, bordered by areolae (0.5 OD in diameter) that converge ventrally just below propodeal pit; outside of areolate borders of metapostnotum on posterior propodeal surface a small glabrous zone of about 1 OD in width; lateral and ventral borders of posterior surface strongly areolate; lateral surface of propodeum dorsoventrally striate, integument between striae smooth. Metasomal terga and sterna faintly imbricate.

Coloration not well preserved; however,

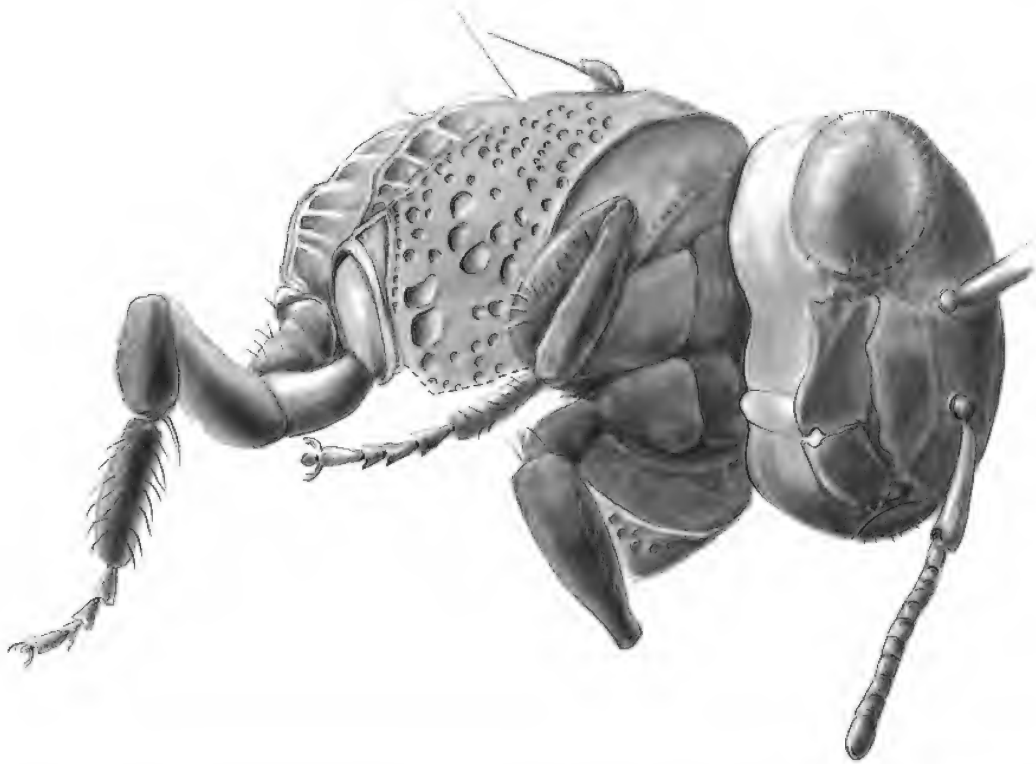


Fig. 33. Right ventrolateral oblique view of head and mesosoma of holotype female of *Glyptapis disareolata,* new species.

where evident, dark brown and without maculations. Wing membrane hyaline; veins strong and dark brown.

Mandible with minute, simple, subappressed setae, longer on ventral border. Clypeus with minute, appressed, simple setae not obscuring integument, such setae also on face below level of antennal sockets. Widely scattered, longer, erect setae on face, clypeus, and supraclypeal area; appressed, minute se-

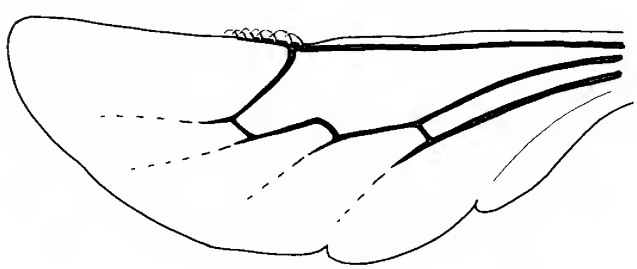
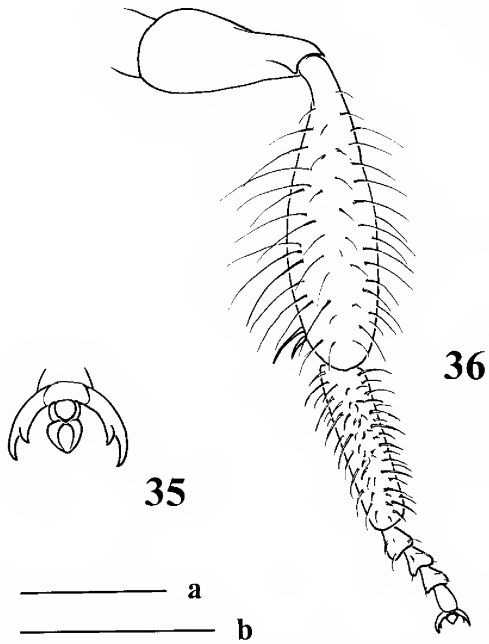


Fig. 34. Hind wing of holotype female of *Glyptapis disareolata,* new species. Scale bar = 1 mm.



Figs. 35–36. Leg structures of *Glyptapis* species. **35.** Claw and arolium of *Glyptapis disareolata,* new species. **36.** Metafemur, metatibia, and metatarsus of female of *Glyptapis fuscula* Cockerell. Scale bars = 0.5 mm (a), 0.25 mm (b); (a = fig. 36; b = fig. 35).

tae disappearing by supraclypeal area; face with longer erect setae intermixed with short, suberect setae; vertex with long, erect setae, each bearing a few minute branches. Gena with similar setae as those of vertex, although shorter, subappressed (not obscuring integument), and simple. Postgena with long, erect, widely scattered setae. Pronotum with scattered, minute, simple setae, appressed but not obscuring the integument except on pronotal lobe setae dense and short and along dorsal carina setae short, erect, and each with a few minute branches. Mesoscutum with short, plumose setae arising out of large, deep punctures, also with minute, sparse setae in interspaces between punctures. Tegula with minute, appressed, simple setae not obscuring integument. Scutellum with pubescence as on mesoscutum except setae slightly longer. Metanotum with minute, erect, simple setae widely scattered. Preëpisternal area without pubescence; setae of mesepisternum (posterior to omaular carina) as on mesoscutum; metepisternum with scattered, short, simple setae. Basal area and posterior surface of propodeum without pubescence; lateral surface of propodeum with pubescence as described for metepisternum. Pubescence of legs generally simple and short except those setae of tarsi long; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with numerous, somewhat long, setae on all surfaces, most of those on inner surface simple but a few with minute branches, those of outer surface with several, short branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

MATERIAL: Two specimens. **Holotype.** Female, B-JH 104 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Glyptapis disareolata* Engel".

Paratype. Female, B-W 156 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Paratype, *Glyptapis disareolata* Engel".

ETYMOLOGY: The specific epithet is a combination of the Latin words *dis* (meaning "without") and *areolatus* (meaning "small spaces") and is a reference to the absence of areolae in the precoxal triangle.

Glyptapis densopunctata, new species

Figure 37
Plate 3b

DIAGNOSIS: This species is most similar to *G. disareolata*; both species have the deep, crater-like punctures of the scutellum restricted to the posterior two-thirds and dense punctures on the metanotum. These characters serve to separate both *G. densopunctata* and *G. disareolata* from *G. fuscula. Glyptapis densopunctata* differs from *G. disareolata* by the presence of areolae in the precoxal triangle.

DESCRIPTION: **Female.** Total body length 6.29 mm; forewing length 4.30 mm. Head slightly wider than long (length 1.72 mm, width 1.84 mm). Upper interorbital distance 1.19 mm; lower interorbital distance 0.88 mm. Interocellar distance 0.38 mm; ocello-

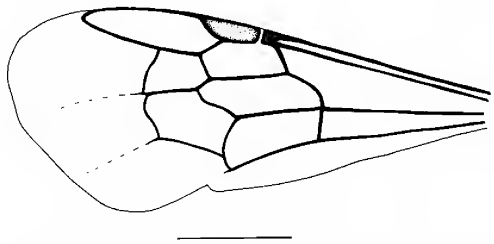


Fig. 37. Forewing of holotype female of *Glyptapis densopunctata,* new species. Scale bar = 1 mm.

cular distance 0.31 mm; median to lateral ocellus 0.13 mm. Intertegular distance 1.38 mm. Basal vein confluent with cu-a; first submarginal cell longer than second; 1m-cu enters second submarginal cell about four times vein width distad of second abscissa of Rs; 2rs-m distad 2m-cu by two times vein width; second submarginal cell gently narrowed anteriorly; 2rs-m gently curved; cu-a long; inner margin of pterostigma in first submarginal cell longer than width of pterostigma; inner margin of pterostigma in marginal cell gently convex; marginal cell apex acutely rounded, offset from wing margin by width of vein, not appendiculate (fig. 37); eight distal hamuli, arranged in a single, evenly spaced series.

Integument generally shining. Mandible with minute punctures separated by 1–2 times a puncture width, integument between smooth. Clypeus with minute punctures separated by 1–2 times puncture width, integument between smooth. Supraclypeal area sculptured as on clypeus. Face and vertex with minute punctures, more well-defined than those of clypeus and supraclypeal area, punctures separated by a puncture width, integument between smooth. Gena and postgena with minute punctures separated by a puncture width, integument between smooth. Pronotum with minute punctures separated by a puncture width, also with minute, transverse striae running along posterior edge of lateral ridge, integument between smooth. Mesoscutum strongly punctured; punctures moderately large (ca. 1/3 OD) and deep, separated by less 0.5–2 times puncture width, integument between such punctures smooth, with minute punctures separated by 1–2 times their own diameter; anterior border of mesoscutum with deeper punctures closely packed. Tegula with minute punctures separated by a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum except deep punctures restricted to posterior two-thirds. Metanotum with minute punctures separated by a puncture width or less, integument between (where evident) smooth. Preëpisternal area (here used for anterior-facing surface of mesepisternum anterior to omaular carina: preepisternal suture is absent, as in other long-tongued bees) with minute punctures separated by a puncture width, integument between smooth. Mesepisternum coarsely reticulate-areolate, integument inside areolae smooth; precoxal triangle anteriorly separated from remainder of mesepisternum by narrow glabrous margin that is less than 0.5 times areola diameter in width, precoxal triangle with weak transverse striae forming dorsoventral row of areolae. Metepisternum transversely striate, integument between striae smooth. Basal area of propodeum strongly areolate, areolae 1 OD or more in diameter, basal area two areolae in length and eight areolae wide; lateral surface of propodeum dorsoventrally striate, integument between striae smooth. Metasomal terga and sterna faintly imbricate.

Color not entirely preserved; however, where evident, dark brown and without maculations. Wing membrane hyaline; veins strong and dark brown.

Mandible with minute, simple, subappressed setae, longer on ventral border. Clypeus with minute, appressed, simple setae not obscuring integument, such setae also on face below level of antennal sockets. Widely scattered, longer, erect setae on face, clypeus, supraclypeal area; appressed, minute setae disappearing by supraclypeal area; face with longer erect setae intermixed with short, suberect setae; vertex with long, erect setae, each bearing a few minute branches. Gena with similar setae as those of vertex, although shorter, subappressed (not obscuring integument), and simple. Postgena with long, erect, widely scattered setae. Pronotum with scattered, minute, simple setae, appressed but not obscuring the integument except on pronotal lobe setae dense and short and along dorsal carina setae short, erect, and each with

a few minute branches. Mesoscutum with short, plumose setae arising out of large, deep punctures, also with minute, sparse setae in interspaces between punctures. Tegula with minute, appressed, simple setae not obscuring integument. Scutellum with pubescence as on mesoscutum except setae slightly longer. Metanotum with minute, erect, simple setae widely scattered. Preëpisternal area without pubescence; setae of mesepisternum (posterior to omaular carina) as on mesoscutum; metepisternum with scattered, short, simple setae. Basal area and posterior surface of propodeum without pubescence; lateral surface of propodeum with pubescence as described for metepisternum. Pubescence of legs generally simple and short except those setae on tarsi long; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with numerous, somewhat long setae on all surfaces, most of those on inner surface simple but a few with minute branches, those of outer surface with several short branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

MATERIAL: Four specimens. **Holotype.** Female, B-W 161 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Glyptapis densopunctata* Engel".

Paratype. Female, B-JH 89 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Paratype, *Glyptapis densopunctata* Engel".

Paratype. Female, Nr. 2623 (CCGG) labeled: "Nr. 2623" // "Paratype, *Glyptapis densopunctata* Engel".

Paratype. Female, Nr. 857 (CHFG) labeled: "Nr. 857, Balt. Bernstein" // "Paratype, *Glyptapis densopunctata* Engel".

ETYMOLOGY: The specific epithet is a combination of the Latin words *densus* (meaning "dense") and *punctatum* (meaning "punctures") and is a reference to the dense punctures of the metanotum.

Glyptapis fuscula Cockerell

Figures 36, 38, 39

Plate 3a

Glyptapis fuscula Cockerell, 1909b: 17.

Glyptapis reticulata Cockerell, 1909b: 16. NEW SYNONYMY.

Glyptapis reducta Cockerell, 1909b: 18. NEW SYNONYMY.

Glyptapis neglecta Salt, 1931: 136. NEW SYNONYMY.

Dasypoda sp. Gerlach, 1989: 253. [misidentification; = *G. reducta* Cockerell]

DIAGNOSIS: This species is similar to *G. densopunctata* and *G. disareolata* but has the deep, crater-like punctures not restricted to the posterior two-thirds of the scutellum and the punctures of the metanotum more widely spaced.

DESCRIPTION: **Female.** Total body length 7.04 mm; forewing length 4.32 mm. Head slightly wider than long (length 1.76 mm, width 1.80 mm). Upper interorbital distance 1.20 mm; lower interorbital distance 0.84 mm. Interocellar distance 0.40 mm; ocellocular distance 0.28 mm; median to lateral ocellus 0.16 mm. Intertegular distance 1.64 mm. Basal vein confluent with cu-a; first submarginal cell longer than second; 1m-cu enters second submarginal cell about eight times vein width distad second abscissa of Rs; 2rs-m distad 2m-cu by vein width; second submarginal cell gently narrowed anteriorly; 2rs-m gently curved; inner margin of pterostigma in first submarginal cell longer than width of pterostigma; inner margin of pterostigma in marginal cell gently convex; marginal cell apex acutely rounded, offset from wing margin by width of vein, not appendiculate; six distal hamuli, arranged in a single, evenly spaced series.

Integument generally shining. Mandible with minute punctures separated by 1–2 times a puncture width, integument between smooth. Clypeus with minute punctures separated by 1–2 times puncture width, integument between smooth. Supraclypeal area sculptured as on clypeus. Face and vertex with minute punctures, more well-defined than those of clypeus and supraclypeal area, punctures separated by a puncture width, integument between smooth. Gena and postgena with minute punctures separated by a puncture width, integument between smooth. Pronotum with minute punctures separated by a puncture width, also with minute, transverse striae running along posterior edge of lateral ridge, integument between smooth. Mesoscutum strongly punctured; punctures moderately large (ca. 1/3 OD) and deep, sep-

Fig. 38. Dorsolateral view of mesosoma of holotype female of *Glyptapis fuscula* Cockerell.

arated by less 0.5–2 times puncture width, integument between such punctures smooth, with minute punctures separated by 1–2 times their own diameter; anterior border of mesoscutum with deeper puncture closely packed (fig. 38). Tegula with minute punctures separated by a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum, deep, crater-like punctures on all parts of scutellum (not restricted to posterior two-thirds). Metanotum with minute punctures separated by 2–3 times puncture width, integument between smooth. Preëpisternal area (here used for anterior-facing surface of mesepisternum anterior to omaular carina: preepisternal suture is absent, as in other long-tongued bees) with minute punctures separated by a puncture width, integument between smooth. Mesepisternum coarsely reticulate-areolate, integument inside areolae smooth; precoxal triangle anteriorly separated from remainder of mesepisternum by narrow glabrous margin that is less than one-half times areola diameter in width, precoxal triangle without strong areolae, instead with weak longitudinal striae that extend only one-half of precoxal triangle. Metepisternum transversely striate, integument between striae smooth. Basal area of propodeum strongly areolate, areolae easily 1 OD in diameter, basal area two areolae in length and eight areolae wide; metapostnotum smooth and impunctate, bordered by areolae (0.5 OD in diameter) that converge ventrally just below propodeal pit; small glabrous zone of about 1 OD in width appearing outside of areolate borders of metapostnotum on posterior propodeal surface; lateral and ventral borders of posterior surface strongly areolate; lateral surface of propodeum dorsoventrally striate, integument between striae smooth. Metasomal terga and sterna faintly imbricate.

Color dark brown without maculations. Wing membrane hyaline; veins dark brown.

Mandible with minute, simple, subappressed

Fig. 39. Lateral view (posterior portion of head in lower right-hand corner) of mesosoma of holotype female of *Glyptapis fuscula* Cockerell. Mesepisternum sculpturing in focus; precoxal triangle cannot be seen in this image.

setae, longer on ventral border. Clypeus with minute, appressed, simple setae not obscuring integument, such setae also on face below level of antennal sockets. Widely scattered, longer, erect setae on face, clypeus, supraclypeal area; appressed, minute setae disappearing by supraclypeal area, replaced on upper face by aforementioned longer, erect setae although now more numerous, such setae long on vertex and each bearing a few minute branches. Gena with similar setae as those of vertex although shorter, subappressed (not obscuring integument), and simple. Postgena with long, erect, widely scattered setae. Pronotum with scattered, minute, simple setae, appressed but not obscuring the integument except on pronotal lobe setae dense and short and along dorsal carina setae short, erect, and each with a few minute branches. Mesoscutum with short, plumose setae arising out of large, deep punctures, also with minute, sparse setae in interspaces between punctures. Tegula with minute, appressed, simple setae not obscuring integument. Scutellum with pubescence as on mesoscutum except setae slightly longer. Metanotum with minute, erect, simple setae widely scattered and a medial patch of long, erect setae, each with a few minute branches. Preëpisternal area without pubescence; setae of mesepisternum (posterior to omaular carina) as on mesoscutum; metepisternum with scattered, short, simple setae. Basal area and posterior surface of propodeum without pubescence; lateral surface of propodeum with pubescence as described for metepisternum. Pubescence of legs generally simple and short except those setae on tarsi long; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with numerous, somewhat long, setae on all surfaces, most

of those on inner surface simple but a few with minute branches, those of outer surface with several, short branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

MATERIAL: Nine specimens. **Holotype (*fuscula*).** Female, K66 (IMGP) labeled: "Holotype, *Glyptapis fuscula* Cockerell" // "Holotype, K66, *Glyptapis fuscula* n. sp. Cockerell, Geologisch-Paläontologisches Institut und Museum, Göttingen" // "*Glyptapis fuscula*" // "*Glyptapis fuscula* Cock. [=Cockerell], K66".

Neotype (*reticulata*; here designated). Female, B-JH 78 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Neotype, *Glyptapis reticulata* Cockerell" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel".

Holotype (*reducta*). Female, G4668 (IMGP) labeled: "Holotype, *Glyptapis reducta* Cockerell" // Holotype, G4668, *Glyptapis reducta* n. sp. Cockerell" // Reservierte Registiernummer, *Dasypoda*: G4668 [Gerlach handwriting]" // "*Dasypoda* sp. indet., Gerlach, J., 1987" // "*Glytapis fuscula* Cockerell, det. M. S. Engel". The eye setae are difficult to see but present. The coarse sculpturing, although also difficult to view through the fine layer of Schimmel on the specimen, can be seen.

Neotype (*neglecta*; here designated). Female B-JH 78 (AMNH) labeled: "Neotype, *Glyptapis neglecta* Salt, desig. M. S. Engel" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel" (see Comments below). This is the same specimen designated as the neotype of *G. reticulata* and thus all other labels are identical with those listed above.

Non-type. Female (ZMUC) labeled: "Apoidea, A. Henningsen, 9–9, 1974" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel". This is the specimen figured by Poinar (1994: 75).

Non-type. Female, B-W 155 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Glyptapis fuscula*? Cockerell, det. M. S. Engel".

Non-type. Female, MB.I.1936 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1936 (No. 18) // "18" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel, 1999".

Non-type. Female, MB.I.1937 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1937, Slg. Berendt" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel".

Non-type. Female, Nr. 1015 (CHMG) labeled: "Nr. 1015" // "*Glyptapis fuscula* Cockerell, det. M. S. Engel".

Non-type. Female (CFEG) labeled: "*Glyptapis fuscula* Cockerell, det. M. S. Engel".

COMMENTS: Salt's description of *G. neglecta* agrees with *G. fuscula* in every respect, particularly the sculpturing of the mesoscutum. Salt considered the distinguishing feature between his specimen and *G. fuscula* to be the hyaline wing membrane in his species; however, the surviving holotype of *G. fuscula* does not actually have fuscous wing membranes. I therefore consider *G. neglecta* and *G. fuscula* to be conspecific. The holotype of *G. neglecta,* however, has since become lost (it was originally in the ill-fated Königsberg collection). I, therefore, here designate a neotype of a specimen from the AMNH collection which agrees with Salt's description. Acting as first reviser (ICZN, 1999b: Art. 24.2) I have chosen *G. fuscula* as the valid name for this taxon and consider *G. reducta* and *G. reticulata,* both published in the same article, to be junior synonyms.

Gerlach (1989) misidentified the holotype of *G. reducta* as a species of the melittid genus *Dasypoda* (Melittidae: Dasypodainae). There is a thin layer of mold over most of the specimen but the punctures of the mesosoma can be easily seen through and within gaps of the mold. There is absolutely no resemblance between *G. reducta* (nor any *Glyptapis* for that matter) and species of *Dasypoda.*

Glyptapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female, MB.I.1944 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1944" // "*Glyptapis* sp. indet., det. M. S. Engel".

Glyptapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female, Nr. 577/1 (CHFG) labeled: "Nr. 577/1, Bittf. [Bitterfeld] Bernstein" // "*Glyptapis* sp. indet., det. M. S. Engel".

Genus *Ctenoplectrella* Cockerell

Ctenoplectrella Cockerell, 1909a: 314. Type species: *Ctenoplectrella viridiceps* Cockerell, 1909a, monobasic. Cockerell, 1909b: 19. Zeuner and Manning, 1976: 172.

DIAGNOSIS: Among Baltic amber Megachlinae *Ctenoplectrella* is most similar to *Glaesosmia* but differs by the longer supraclypeal area, narrow gena, and more orthogonal second abscissa of Rs.

DESCRIPTION: Mandible with three teeth along apical margin, upper tooth separated from lower two teeth by a short, gently concave cutting-edge (fig. 40). Malar space short, much shorter than basal mandibular width. Clypeus flat; not extending below lower tangent of compound eyes (fig. 40). Hypostomal ridge carinate, anterior angle rounded. Subantennal sutures longer than antennal socket diameter. Compound eyes bare (fig. 40); compound eye broader than gena in lateral view; inner margins straight and slightly converging below. F1 slightly longer than F2; length of F2 approximately equal to that of F3. Posterior margin of vertex gently concave. Preoccipital area rounded. Mesoscutum and scutellum not coarsely sculptured; mesoscutal anterior border broadly rounded (fig. 45); median line moderately impressed; parapsidal lines faintly impressed and linear; tegula oval; scutellum low, weakly convex, not overhanging metanotum, anterior margin without notches; metanotum slightly inclined but generally not far off from horizontal (fig. 46); anterior and posterior borders of metepisternum converging ventrally and meeting one another at point of mesocoxal base; propodeum not strongly sculptured. Claws with inner tooth, inner tooth shorter than outer (fig. 42); arolium present (fig. 42); outer apex of mesotibia without spine; two metatibial spurs, spurs serrate. Basal vein strongly arcuate; second abscissa Rs approximately orthogonal to M (figs. 41, 43). No apparent maculations on integument.

COMMENTS: This genus has long been associated with the apine genera *Ctenoplectra* Kirby (*In* Kirby and Spence, 1826) and *Ctenoplectrina* Cockerell (1930b), together forming the tribe Ctenoplectrini. Oddly, the unity of *Ctenoplectrella* with Ctenoplectrini seems to be simply based upon two entirely unfounded criteria, **1.** the name chosen by Cockerell (1909a), which suggests some affinity between the groups (*Ctenoplectrella* is a diminutive form of *Ctenoplectra*); and **2.** an anecdotal comment by Cockerell (1909b) who said (p. 13), "Their [*Glyptapis* and *Ctenoplectrella*] nearest relative in the modern fauna appears to be *Ctenoplectra*...," but provided no characters to support such a relationship. Indeed, the wing venation of *Ctenoplectrella* shares a superficial similarity to that of some Ctenoplectrini. Unfortunately, the similarity between the two groups ends at this point (detailed above and further below). The Ctenoplectrini was originally proposed as a family by Cockerell (1930a), later moved into the Melittidae as a subfamily (Michener, 1944), resurrected as a family intermediate between short- and long-tongued bees by Michener and Greenberg (1980), only to be later recognized as a de-

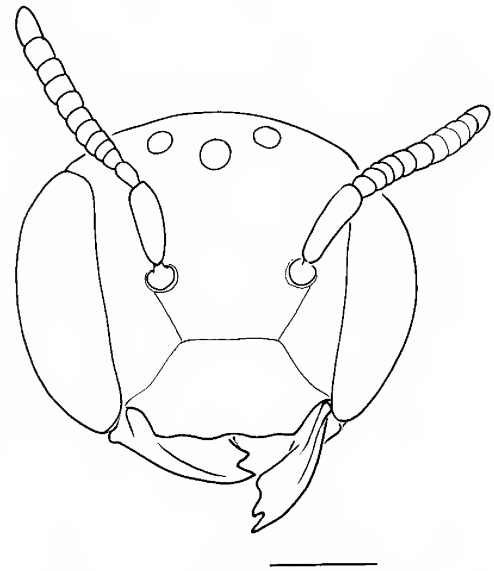


Fig. 40. Frontal view of head of neotype female of *Ctenoplectrella viridiceps* Cockerell. Scale bar = 1 mm.

rived group of Apinae where it is currently placed (Roig-Alsina and Michener, 1993; Michener, 2000a). The placement of *Ctenoplectrella* has generally followed that of *Ctenoplectra* (e.g., Zeuner and Manning, 1976; Michener and Greenberg, 1980), once again, presumably owing to the common derivation of their names and Cockerell's comment rather than any shared characteristics. Zeuner and Manning (1976) followed Cockerell's assertion of affinity with *Ctenoplectra* and placed *Ctenoplectrella* and *Glyptapis* in Ctenoplectrinae, at that time in the Melittidae (sensu Michener, 1944). It is, unfortunately, apparent that neither of these authors had actually seen specimens of the latter two genera. For instance, Zeuner and Manning (op. cit.) characterize these groups as having the inner metatibial spur modified as in *Ctenoplectra*; namely, broadened basally with numerous, elongate teeth, as well as having a pygidial plate in females. Although the holotype for *Ctenoplectrella* is lost (a neotype is designated below), the types of *Glyptapis* have survived in the Institut und Museum für Geologie und Paläontologie, Göttingen and none of these characters are present in *Glyptapis* (nor in the neotype of *Ctenoplectrella*). Moreover, these distinctive characters are never once mentioned by Cockerell (1909b) who was quite adept and would undoubtedly have noticed these peculiar features. Zeuner and Manning (1976) do not provide descriptions for these taxa, instead referring to the original works, once again suggesting that Zeuner and Manning did not have the opportunity to see specimens of these taxa before their untimely deaths. The type of *Ctenoplectrella viridiceps* was certainly not available to Zeuner and Manning since it was lost during World War II. The specimen here considered as the neotype for *Ctenoplectrella* agrees in every respect with Cockerell's description and, of particular importance, with his figures (especially in the shape of the pterostigma, which is quite distinctive). I am therefore confident that the *Ctenoplectrella* of Cockerell is the same as my own.

Ctenoplectrella differs from Ctenoplectrini (Apidae) by the flat clypeus (not bent posteriorly at the apicolateral margins), the coarsely serrate inner metatibial spur, the absence of a pygidial plate, the broadened mandible that is reminiscent of the Megachilinae, the presence of a true metasomal scopa, the strongly arcuate basal vein, the absence of hairs on the metapostnotum, and the absence of a metabasitibial plate, among numerous other characters.

The absence of a preepisternal groove, the shortened jugal lobe, and the fully exposed mesocoxa are all characteristic of Melittidae + long-tongued bees, while most Apidae have the lateral portions of the clypeus strongly bent posteriorly, a feature absent in Megachilidae and Melittidae (as well as *Ctenoplectrella* and *Glyptapis*; unobservable for *Glaesosmia*). Among the Megachilinae, however, *Ctenoplectrella* is remarkable for the slanting metanotum and the broad labrum (the latter plesiomorphic trait shared with *Glyptapis*).

Key to Species of *Ctenoplectrella*

1. Crossvein 2rs-m strongly and doubly arcuate, thus second submarginal cell more strongly produced toward wing apex along its posterior margin (fig. 43); medioapical margin of clypeus straight 2
– Crossvein 2rs-m relatively straight and therefore second submarginal cell not more strongly produced toward wing apex along its posterior margin (fig. 41); medioapical margin of clypeus gently convex (fig. 40) . . . . . *C. viridiceps* Cockerell
2. Mesoscutum and scutellum punctate . . . . . *C. cockerelli,* n. sp.
– Mesoscutum and scutellum impunctate . . . . . *C. grimaldii,* n. sp.

Ctenoplectrella viridiceps Cockerell

Figures 40–42
Plate 3c–e

Ctenoplectrella viridiceps Cockerell, 1909a: 314.
Ctenoplectrella dentata Salt, 1931: 139. NEW SYNONYMY.
Ctenoplectrella splendens Kelner-Pillault, 1970a: 13. NEW SYNONYMY.

DIAGNOSIS: This species is distinguished by the gently concave mediapical margin of the clypeus (fig. 40) and weakly arcuate 2rs-m (fig. 41).

DESCRIPTION: **Female.** Total body length 5.85 mm; forewing length 3.06 mm. Head slightly wider than long (length 1.53 mm, width 1.88 mm). Upper interorbital distance

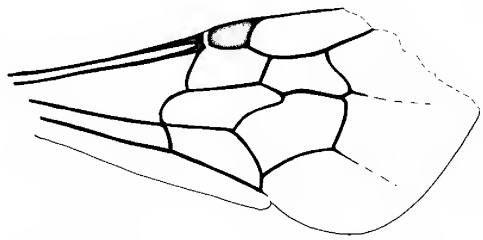


Fig. 41. Forewing of neotype female of *Ctenoplectrella viridiceps* Cockerell. Scale bar = 1 mm.

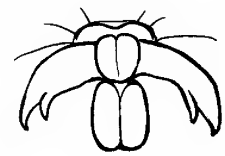


Fig. 42. Claw and arolium of neotype female of *Ctenoplectrella viridiceps* Cockerell. Scale bar = 0.25 mm.

1.16 mm; lower interorbital distance 1.00 mm. Interocellar distance 0.44 mm; ocellocular distance 0.33 mm; median ocellus to lateral ocellus 0.16 mm. Median and parapsidal lines moderately impressed, parapsidal lines elongate (not punctiform). Intertegular distance 1.31 mm. Basal vein confluent with cu-a; second abscissa Rs basad 1m-cu by 6.5 times vein width; 2rs-m distad 2m-cu by two times vein width, 2rs-m relatively straight, arching only toward its apex before meeting vein M; second submarginal cell slightly longer than first submarginal cell; six distal hamuli arranged in a single, evenly spaced series.

Outer surface of mandible with minute punctures separated by a puncture width or less, integument between smooth. Clypeus with faint, coarse punctures separated by a puncture width or less, integument between smooth. Supraclypeal area and face with punctures more well-defined than those of clypeus and separated by 1–2 times puncture width, integument between smooth. Vertex and gena with sculpturing as on face although punctures slightly more closely spaced, separated by about a puncture width, integument between smooth. Mesoscutum with small punctures separated by a puncture width or slightly less, integument between smooth. Tegula with minute punctures separated by 1–2 times a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum. Metanotum impunctate and smooth. Preëpisternal area (i.e., anterior-facing surface anterior to omaulus) essentially impunctate and smooth except for a few, exceedingly faint, widely spaced, coarse punctures. Mesepisternum with coarse, slightly faint punctures separated by 1–2 times a puncture width, integument between smooth, punctures becoming somewhat fainter ventrally and posteriorly. Metepisternum impunctate and smooth. Propodeum (basal, lateral, and posterior surfaces) finely imbricate. Terga with minute, faint punctures separated by 1–3 times a puncture width, integument between finely imbricate; sterna imbricate.

Coloration dark brown without maculations. Wing membrane hyaline except between C and Sc+R slightly fuscous in some specimens; veins strong and dark brown.

Mandible with minute, simple, appressed setae. Clypeus with minute, appressed, simple setae not obscuring integument; similar setae also on face below level of antennal sockets, intermixed with scattered, longer, erect setae on face, clypeus, supraclypeal area, gena, and postgena. Mesoscutum and scutellum with scattered, short, simple setae except those of scutellum slightly longer. Pleural pubescence as described for mesoscutum. Basal area of propodeum without pubescence; lateral and posterior surfaces with pubescence as described for mesoscutum. Pubescence of legs generally simple and short; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with scattered, simple, moderate-length setae, a few with minute branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

Male. As described for the female except

as indicated: Total body length 6.93 mm; forewing length 4.00 mm. Head slightly wider than long (length 1.70 mm, width 1.86 mm). Upper interorbital distance 1.10 mm; lower interorbital distance 1.00 mm. Interocellar distance 0.40 mm; ocellocular distance 0.31 mm; median ocellus to lateral ocellus 0.17 mm. Intertegular distance 1.45 mm. Flagellum elongate, reaching to posterior margin of mesoscutum; F1 longer than F2; F2 equal in length to F3. T6 deeply bifid at apex and slightly protuberant. Metasomal scopa absent.

MATERIAL: Ten specimens. **Neotype (*viridiceps*; here designated).** Female, B-JH 95 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Neotype, *Ctenoplectrella viridiceps* Cockerell, desig. M. S. Engel".

Neotype (*dentata*; here designated). Male, NB.I.1949 (ZMHB) labeled: "Neotype, *Ctenoplectrella dentata* Salt, desig. M. S. Engel". This is the same as specimen as the holotype for *C. splendens* and therefore the remaining labels of the specimen are given below under *C. splendens.*

Holotype (*splendens*). Male, NB.I.1949 (ZMHB) labeled: "49" // "*Ctenoplectrella splendens,* Holotype, S. Kelner-Pillault det." // "Holotyp [sic], Paläontologisches Museum Berlin, *Ctenoplectrella splendens* Kelner-Pillault, 1970, Baltischer Bernstein" // "Holotype, *Ctenoplectrella splendens* Kelner-Pillault".

Non-type. Female, B-JH 93 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female, B-JH 83 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female, B-W 158 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Ctenoplectrella viridiceps*? Cockerell, det. M. S. Engel".

Non-type. Female, MB.I.1940 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1940 (No. 29)" // "29" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female, MB.I.1941 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1941 (No. 17)" // "17" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female, Nr. 24 (CFKG) labeled: "1987, Nr. 24" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female (CJVG) labeled: "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

Non-type. Female, Nr. 1615 (CCGG) labeled: "Nr. 1615" // "*Ctenoplectrella viridiceps* Cockerell, det. M. S. Engel".

COMMENTS: The species was proposed as new again by Cockerell (1909b) but the name was already made available by Cockerell (1909a).

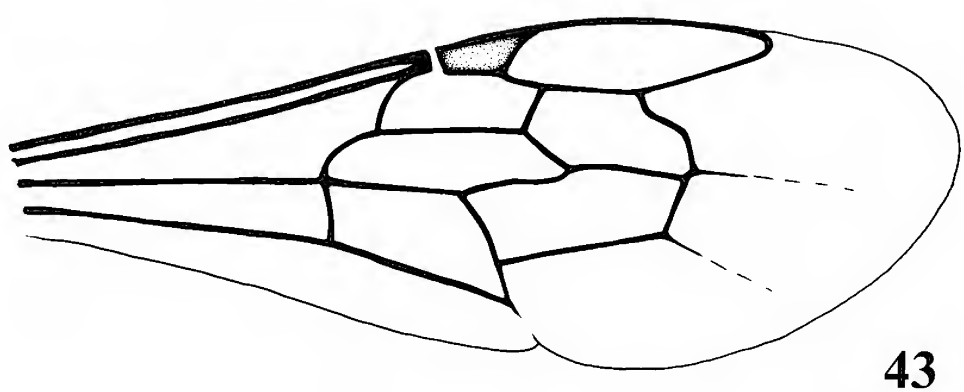
The specimen here designated as the neotype agrees with Cockerell's original description and figures, particularly in the shape of the pterostigma. Zeuner and Manning (1976) indicate the holotype to have been moved to the Museum für Naturkunde, Humboldt-Universität, Berlin, but upon inspection of their collection I failed to find any specimens from the Königsberg collection. Most material from the former Königsberg collection eventually ended up in the Institut und Museum für Geologie und Paläontologie, Göttingen, where some of Cockerell's other types were discovered (e.g., those of *Glyptapis*), but *Ctenoplectrella* was not among them. *Ctenoplectrella* was cataloged in the Göttingen collection as specimen "K65" but it was not to be found. I therefore consider the holotype to have been lost and here designate a neotype.

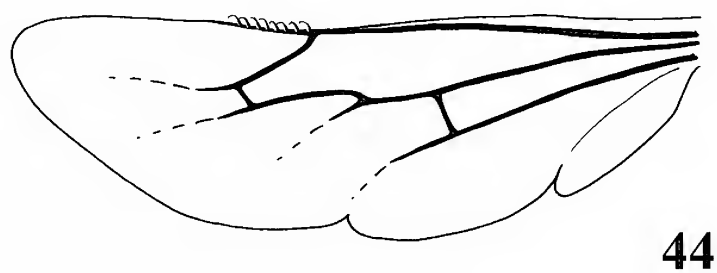
The species proposed by Salt (1931), a male of *Ctenoplectrella,* is undoubtedly the male for *C. viridiceps.* The neotype of *C. splendens* in Berlin is the only existing male specimen (of any genus!) preserved in Baltic amber.

***Ctenoplectrella cockerelli*,** new species

Figures 43, 44

DIAGNOSIS: This is most similar to *C. grimaldii* (see below) in the strongly produced second submarginal cell (fig. 43), straight clypeal apex, and narrow gena but differs by





Figs. 43–44. Wings of holotype female of *Ctenoplectrella cockerelli,* new species. **43.** Forewing. **44.** Hind wing. Scale bar = 1 mm.

the presence of punctures on the mesoscutum and scutellum (absent in *C. grimaldii*).

DESCRIPTION: **Female.** Total body length 5.35 mm; forewing length 3.65 mm. Head slightly wider than long (length 1.56 mm, width 1.78 mm). Upper interorbital distance 1.13 mm; lower interorbital distance 0.97 mm. Interocellar distance 0.31 mm; ocellocular distance 0.31 mm; median ocellus to lateral ocellus 0.13 mm. Intertegular distance 1.28 mm. Basal vein confluent with cu-a; second abscissa of Rs basad 1m-cu by seven times vein width; 2rs-m distad 2m-cu by vein width, 2rs-m doubly arcuate; second submarginal cell slightly longer than first submarginal cell; eight distal hamuli, arranged in a single, evenly spaced series (fig. 44).

Outer surface of mandible with minute punctures separated by a puncture width or less, integument between smooth. Clypeus with small punctures separated by a puncture width or less, integument between smooth. Supraclypeal area sculptured as on clypeus. Face with punctures separated by 1–1.5 times a puncture width, integument between smooth. Vertex and gena with small punctures separated by about a puncture width, integument between smooth. Mesoscutum with small punctures separated by a puncture width or slightly less, integument between smooth. Tegula with minute punctures separated by a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum. Metanotum impunctate and smooth. Preëpisternal area (i.e., anterior-facing surface anterior to omaulus) essentially impunctate and smooth except for a few, exceedingly faint, widely spaced, coarse punc-

tures. Mesepisternum with coarse, slightly faint punctures separated by a puncture width, integument between smooth, punctures becoming somewhat fainter ventrally and posteriorly. Metepisternum impunctate and smooth. Propodeum (basal, lateral, and posterior surfaces) impunctate and smooth. Terga with small punctures separated by 1–2 times a puncture width, integument between smooth; sterna imbricate.

Color brown without maculations. Wing membrane hyaline; veins strong and dark brown.

Mandible with minute, simple, appressed setae. Clypeus with minute, appressed, simple setae not obscuring integument; similar setae also on face below level of antennal sockets, intermixed with scattered, longer, erect setae on face, clypeus, supraclypeal area, gena, and postgena. Mesoscutum and scutellum with scattered, short, simple setae except those of scutellum slightly longer. Pleural pubescence as described for mesoscutum. Basal area of propodeum without pubescence; lateral and posterior surfaces with pubescence as described for mesoscutum. Pubescence of legs generally simple and short; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with scattered, simple, moderate-length setae, a few with minute branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of bands of dense, long, erect, simple setae.

MATERIAL: Three specimens. **Holotype.** Female, B-W 160 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Ctenoplectrella cockerelli* Engel".

Paratype. Female, MB.I.1942 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1942 (No. 31)" // "31" // "Paratype, *Ctenoplectrella cockerelli* Engel".

Paratype. Female, Nr. 1011 (CCGG) labeled: "Nr. 1011" // "Paratype, *Ctenoplectrella cockerelli* Engel".

ETYMOLOGY: The specific epithet is a patronymic honoring the late Prof. Theodore D. A. Cockerell (1866–1948). Cockerell was the first to critically examine the Baltic amber bees and to attempt to place them into a phylogenetic context. Weber (1965, 2000) has presented a bibliography of Cockerell's papers as well as a sampling of his published writings on topics ranging from entomology to philosophy.

***Ctenoplectrella grimaldii*, new species**

Figures 45, 46
Plate 3f

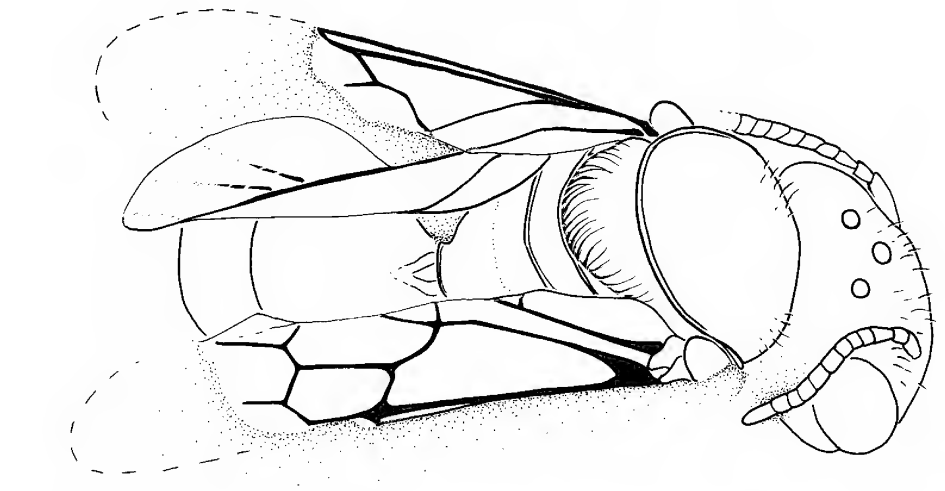
DIAGNOSIS: Refer to diagnosis presented for *C. cockerelli* (above).

DESCRIPTION: **Female.** Total body length 5.40 mm; forewing length 3.56 mm. Head slightly wider than long (length 1.34 mm, width 1.72 mm). Upper interorbital distance 1.11 mm; lower interorbital distance 1.00 mm. Interocellar distance 0.34 mm; ocellocular distance 0.31 mm; median ocellus to lateral ocellus 0.16 mm. Intertegular distance 1.13 mm. Basal vein confluent with cu-a; second abscissa of Rs basad 1m-cu by seven times vein width; 2rs-m distad 2m-cu by vein width, 2rs-m doubly arcuate; second submarginal cell slightly longer than first submarginal cell; eight distal hamuli, arranged in a single, evenly spaced series.

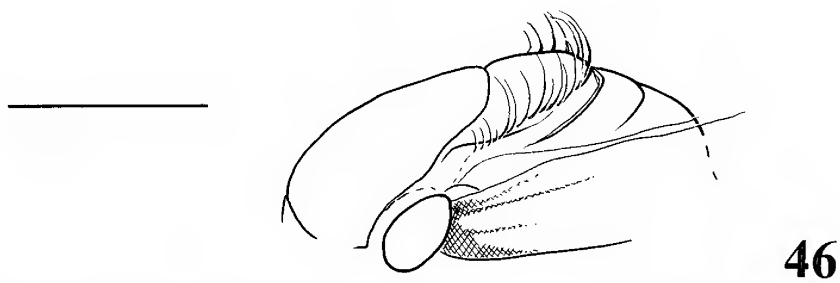
Mandibular sculpturing not visible. Clypeus with small punctures separated by a puncture width or less, integument between smooth. Supraclypeal area sculptured as on clypeus. Face with punctures separated by 1–1.5 times a puncture width, integument between smooth. Vertex and gena with small punctures separated by about a puncture width, integument between smooth. Mesoscutum, scutellum, and metanotum impunctate and finely imbricate. Tegula with minute, faint punctures separated by 1–2 times a puncture width, integument between faintly imbricate. Pleura impunctate and finely imbricate. Propodeum impunctate and imbricate. Terga and sterna imbricate.

Color dark brown or black without maculations. Wing membrane hyaline; veins strong and dark brown.

Mandible with minute, simple, appressed setae. Clypeus with minute, appressed, simple setae not obscuring integument; similar setae also on face below level of antennal sockets, intermixed with scattered, longer,



45



46

Figs. 45–46. Holotype female of *Ctenoplectrella grimaldii,* new species. **45.** Dorsal view of holotype. **46.** Left lateral view of mesosomal dorsum. Scale bar = 1 mm.

erect setae on face, clypeus, supraclypeal area, gena, and postgena. Mesoscutum and scutellum with scattered, short, simple setae except those of scutellum slightly longer. Pleural pubescence as described for mesoscutum. Basal area of propodeum without pubescence; lateral and posterior surfaces with pubescence as described for mesoscutum. Pubescence of legs generally simple and short; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with scattered, simple, moderate-length setae, a few with minute branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

MATERIAL: One specimen. **Holotype.** Female, B-JH 88 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Ctenoplectrella grimaldii* Engel".

ETYMOLOGY: The specific epithet is a patronymic honoring Dr. David A. Grimaldi for his friendship, advice, and assistance with my paleontological studies.

Ctenoplectrella sp. indet.

MATERIAL: One specimen. **Non-type.** Female, Nr. 1616 (CCGG) labeled: "Nr. 1616" // "*Ctenoplectrella* sp. indet., det. M. S. Engel".

COMMENTS: It is possible that this speci-

men represents another individual of *C. viridiceps.*

Ctenoplectrella sp. indet.

MATERIAL: One specimen. **Non-type.** Female, Nr. 3000 (GPUH) labeled: "Nr. 3000" // "*Ctenoplectrella* sp. indet., det. M. S. Engel".

Ctenoplectrella? sp. indet.

Megachile sp. Gerlach, 1989: 255. [misidentification]

MATERIAL: One specimen. **Non-type.** Female, Nr. G4669 (IMGP) labeled "Reservierte Registriernummer, *Megachile*: G4669 [Gerlach handwriting]" // "*Megachile* sp. indet., Gerlach, J., 1987" // "G4669, *Ctenoplectrella* sp. indet. (*sensu* Ckll.), det. M. S. Engel, 1999, Geologisch-Paläontologisches Institut und Museum, Göttingen".

COMMENTS: This specimen is poorly preserved and is mostly covered by Schimmel except for portions of the compound eyes, an exposed wing, apices of the legs; other structures dimly visible through thinner regions of Schimmel. Those few visible features generally suggest a species of *Ctenoplectrella* (i.e., an osmiine without eye setae, relatively orthogonal second abscissa Rs to M, and with an apparently narrow gena). The strongly arcuate 2rs-m suggests *C. cockerelli* or *C. grimaldii* but further identification as to species is impossible. The somewhat larger body size (ca. 8 mm) suggests that the specimen may represent an otherwise unknown species (if indeed it is a true *Ctenoplectrella* at all!). The body size is closer to that of *Glaesosmia.*

***Glaesosmia*,** new genus

TYPE SPECIES: *Glaesosmia genalis* Engel, new species.

DIAGNOSIS: This genus is most similar to *Ctenoplectrella* but differs by the short supraclypeal area, broad gena, angulate second abscissa of Rs (fig. 47), and broad head (refer to key to genera, above).

DESCRIPTION: Mandible with three lower teeth along apical margin, upper tooth separated from lower two teeth by a short, gently concave cutting-edge. Malar space short, much shorter than basal mandibular width. Clypeus flat; not extending below lower tangent of compound eyes. Subantennal sutures as long as antennal socket diameter. Compound eyes bare; compound eye as broad as gena in lateral view; inner margins straight and slightly converging below. F1 slightly longer than F2; length of F2 approximately equal to that of F3. Posterior margin of vertex gently concave. Preoccipital area rounded. Mesoscutum and scutellum not coarsely sculptured; mesoscutal anterior border broadly rounded; median line moderately impressed; parapsidal lines moderately impressed and linear; tegula oval; scutellum low, weakly convex, not overhanging metanotum; propodeum not strongly sculptured. Claws with inner tooth, inner tooth shorter than outer; arolium present; outer apex of mesotibia without spine; two metatibial spurs, spurs serrate. Basal vein strongly arcuate; second abscissa Rs forming an acute angle with M (fig. 47). No apparent maculations on integument.

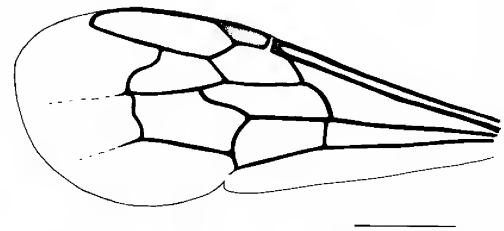


Fig. 47. Forewing of holotype female of *Glaesosmia genalis,* new species. Scale bar = 1 mm.

ETYMOLOGY: The new genus-group name is a combination of *glaesum* (Latin, meaning "amber") and the generic name *Osmia.* The name is feminine.

***Glaesosmia genalis*,** new species

Figure 47

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 7.15 mm; forewing length 5.05 mm. Head much wider than long (length 2.05 mm, width 2.30 mm). Upper interorbital distance 1.50 mm; lower interorbital distance 1.45 mm. Interocellar distance 0.40 mm; ocellocular distance 0.40 mm; median ocellus to lateral ocellus 0.15 mm. Intertegular distance 1.85 mm. Basal vein basad cu-a by vein

width; second abscissa Rs basad 1m-cu by 10 times vein width; 2rs-m distad 2m-cu by vein width, 2rs-m doubly arcuate; second submarginal cell slightly longer than first submarginal cell, lower apical margin of second submarginal cell extending apically; 10 distal hamuli, arranged in a single, evenly spaced series.

Clypeus with small punctures separated by a puncture width or less, integument between smooth. Supraclypeal area and face with small punctures separated by a puncture width or less, integument between smooth. Vertex and gena with sculpturing as on face, although punctures slightly more widely spaced, separated by about 0.5–1.5 times a puncture width, integument between smooth. Mesoscutum with small punctures separated by less than a puncture width, integument between smooth. Tegula with minute punctures separated by a puncture width or less, integument between smooth. Scutellum sculptured as on mesoscutum. Metanotum rugulose. Preëpisternal area (i.e., anterior-facing surface anterior to omaulus) essentially impunctate and smooth except for a few, exceedingly faint, widely spaced, coarse punctures. Mesepisternum with small punctures separated a puncture width, integument between smooth, punctures becoming faint on posterior third. Metepisternum impunctate and smooth. Basal area and posterior surface of propodeum finely imbricate and impunctate, lateral surface finely imbricate with a few, sparse, faint, small punctures. T1–T2 impunctate and smooth; remaining terga with coarse, faint punctures separated by a puncture width, integument between smooth; sternal integument obscured.

Coloration brown, without maculations. Wing membrane hyaline except between C+Sc and R slightly fuscous in some specimens; veins dark brown.

Clypeus with minute, appressed, simple setae not obscuring integument. Face, clypeus, supraclypeal area, gena, and postgena with scattered, short, erect or suberect, simple setae. Mesoscutum and scutellum with scattered, short, simple setae. Pleural pubescence as described for mesoscutum. Basal area of propodeum without pubescence; lateral and posterior surfaces with pubescence as described for mesoscutum. Pubescence of legs generally simple and short; inner surface of metafemur without pubescence, outer, anterior, and posterior surfaces with short, branched setae; metatibia with scattered, simple, moderate-length setae, a few with minute branches. Central discs of metasomal terga with sparse, minute, simple, appressed setae, setae longer and erect to suberect on lateral borders; sternal scopa composed of dense, long, erect, simple setae.

MATERIAL: One specimen. **Holotype.** Female, B-JH 80 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Glaesosmia genalis* Engel".

ETYMOLOGY: The specific epithet is a reference to the enlarged gena (L. *gena,* meaning "cheek").

Family APIDAE Latreille

DIAGNOSIS: Long-tongued bees lacking a strong metasomal scopa in nonparasitic forms and with the clypeus bent posteriorly lateral to the narrowed labral articulation.

DESCRIPTION: Single subantennal suture; suture meeting lower margin of antennal socket. Facial foveae absent. Lower lateral margins of clypeus bent posteriorly on either side of labrum. Flabellum present; glossa acute; labial palpus with first two segments flattened, sheath-like, and elongate; *submentum strongly V-shaped and sclerotized, submental arms articulating with cardines slightly above cardo-stipital articulations.* Galeal comb absent; stipital comb and concavity present; *basistiptial process elongate.* Preëpisternal groove absent. Mesocoxa entirely exposed. Metabasitibial frequently present. Jugal lobe short. Strong metasomal scopa absent; scopa variously formed on metafemur and metatibia, metatibia sometimes developed into a corbicula (in nonparasitic females). Metapostnotum setose. Pygidial plate and fimbria of female typically present.

Key to Subfamilies of Apidae in Baltic Amber

1. Metatibia modified into corbicula; procoxa slightly wider than long or as long as wide; rastellum present (corbiculate Apinae) . . . . . Apinae Latreille
– Metatibia not modified into corbicula, typical scopa present but reduced; procoxa much wider than long; rastellum absent . . . . . Xylocopinae Latreille

Subfamily Xylocopinae Latreille

Xylocopae Latreille 1802b: 379. Type genus: *Xylocopa* Latreille, 1802b.

Diagnosis: Apid bees with distinctly broadened procoxae and a reduced metatibial scopa.

Description: Flabellum set at apex of bare shank (Michener and Brooks, 1984). Procoxae wider than long; metatibial scopa reduced (in nonparasitic females), not developed into corbicula.

Comments: This morphologically diverse subfamily of bees contains the familiar carpenter bees of the genera *Xylocopa* and *Ceratina.* The subfamily is partitioned into four tribes; the Allodapini of the Old World tropics and south temperate regions, the Manueliini of southern South America, and the cosmopolitan tribes Ceratinini (small carpenter bees of the genera *Ceratina* and *Megaceratina*; *Pithitis* is considered a subgenus of *Ceratina* by Michener, 2000a) and Xylocopini (the large carpenter bees of the genus *Xylocopa*; including *Proxylocopa* and *Lestis* according to Minckley, 1998). A key to these four tribes was presented by Sakagami and Michener (1987) and Michener (2000a). Individuals of Ceratinini and Xylocopini have been discovered in various fossil deposits [Heer, 1849, 1865 (as *Bombus*); Cockerell, 1906; Statz, 1936; Zeuner, 1938; Zhang, 1990; Zhang et al., 1994; Engel, in press-a]; however, no Xylocopinae have previously been recorded as amber inclusions. These fossils are also the oldest record of the subfamily. A cladistic study of the subfamily is presented below based on exemplar genera (see Cladistic Analyses), while phylogenetic studies on the relationships within Xylocopini have been undertaken by Minckley (1998) and for Allodapini by Reyes (1998). Species of Manueliini were reviewed by Daly et al. (1987) but relationships were not explored cladistically. No cladogram has yet been produced for Ceratinini.

Boreallodapini, New Tribe

Type Genus: *Boreallodape* Engel, new genus.

Diagnosis: Among xylocopine bees the boreallodapines are most closely related to the tribes Ceratinini and Allodapini; all three have the abruptly narrowed mandible (fig. 54), have the anterior tentorial pit situation near the middle of the clypeus (fig. 49), and have flattened labral surfaces (Xylocopini and Manueliini have tapering mandibles, the anterior tentorial pits situated well above the middle of the clypeus, and basal labral elevations). From the Allodapini the new tribe differs by having an elongate supraclypeal area (longer than the diameter of the antennal sockets) (fig. 49), unflattened distal metasomal terga (figs. 48, 53, 55), the lateral margins of the clypeus concave (not biconvex) (fig. 49), and in the hind wing the first abscissa of M is more than three-quarters the length of the second abscissa of M+Cu (fig. 51). From the Ceratinini the boreallodapines can be distinguished by having only two submarginal cells (fig. 50) and lacking a metabasitibial plate.

Description: Mandible abruptly narrowed near midpoint (fig. 54). Anterior tentorial pits near (frequently slightly above) midpoint of clypeus; lateral margins of clypeus strongly concave (fig. 49). Subantennal sutures longer than antennal socket diameter (i.e., supraclypeal area more elongate than that in Allodapini in which the subantennal sutures are shorter than the diameter of the antennal socket) (fig. 49). Scape short, not reaching to median ocellus; F1 less than combined lengths of F2+F3. Prosternum with short basisternum and anterior process, lateral processes slightly elongate, without constriction between basisternum and furcasternum (figs. 56–58); furcasternum elongate with strong medial groove from apophyseal pit that extends slightly less than three-quarters of total furcasternal length. Claw with strong inner tooth; arolium large (fig. 52). Forewing membrane pubescent, not papillate; marginal cell apex rounded on wing margin (figs. 50, 55); pterostigma of moderate size (not obsolete as in Xylocopini); prestigma short; two submarginal cells (figs. 50, 55); hind wing with first abscissa of M more than three-quarters length of second abscissa of M+Cu (fig. 51); jugal lobe one-half length of vannal lobe. Metabasitibial plate absent. Distal metasomal terga distinctly not flattened dorsally (in Allodapini the distal three metasomal terga are flattened dorsally) (fig. 55); pygidial fimbria absent; pygidial plate absent.

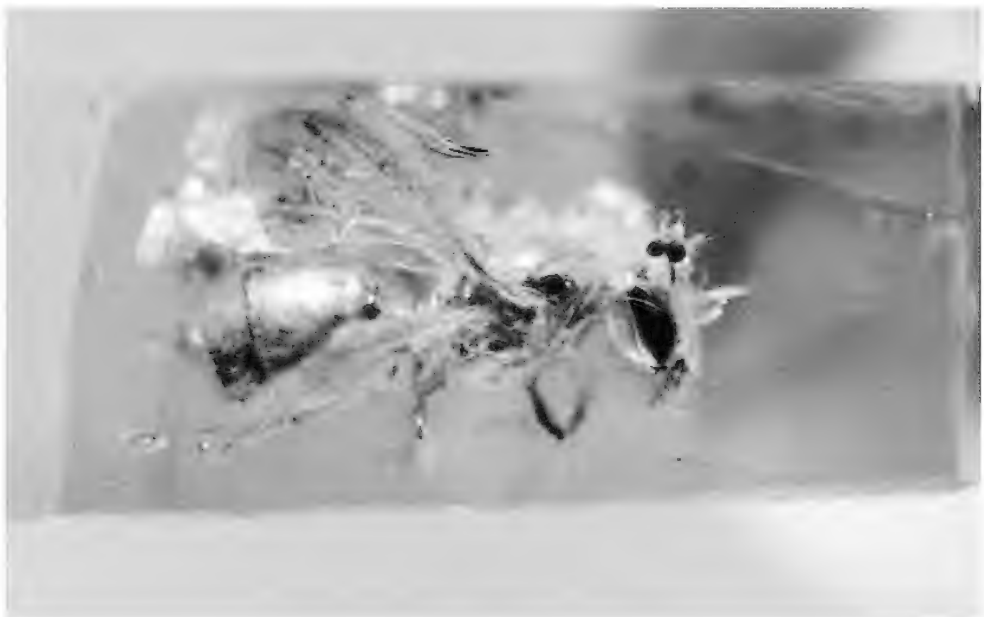


Fig. 48. Right lateral view of holotype female of *Boreallodape baltica,* new species.

***Boreallodape*, new genus**

TYPE SPECIES: *Boreallodape baltica* Engel, new species.

DIAGNOSIS: As for the tribe (see above).

DESCRIPTION: As for the tribe with the following additions: Clypeus not protuberant in lateral view, gently and slightly curved, slightly extending below lower tangent of compound eyes, with scattered, faint punctures; lateroclypeal carina absent; upper clypeal margin relatively straight. Antennal sockets slightly above level of middle of compound eyes. Frons not protuberant. Vertex behind ocelli strongly concave, vertex relatively short. Preoccipital area rounded. Gena narrower than compound eye in lateral view. Malar space short, much less than basal mandibular width. Mandible bidentate (fig. 54). Mesoscutum broadly rounded anteriorly; median and parapsidal lines moderately impressed. Tibial combs absent; coxae without spines or carinae. Wing membrane hyaline; veins dark brown; basal vein strongly curved (figs. 50, 55); pterostigma well developed, margin inside marginal cell slightly convex; apex of marginal cell acutely rounded, set off from wing margin by width of vein at most; second submarginal cell shorter than first; 1rs-m basad of 1m-cu; five distal hamuli arranged in a single, evenly spaced series.

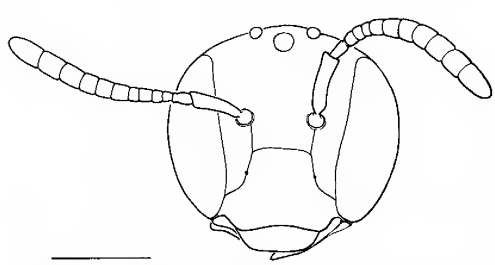
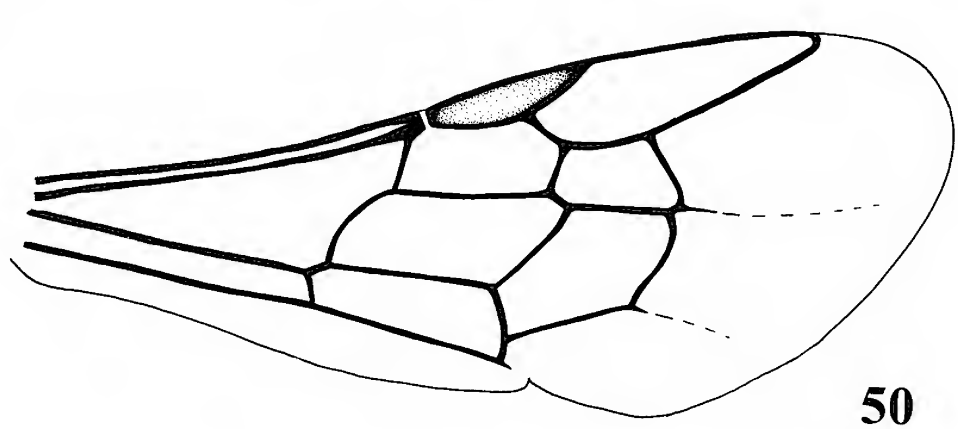
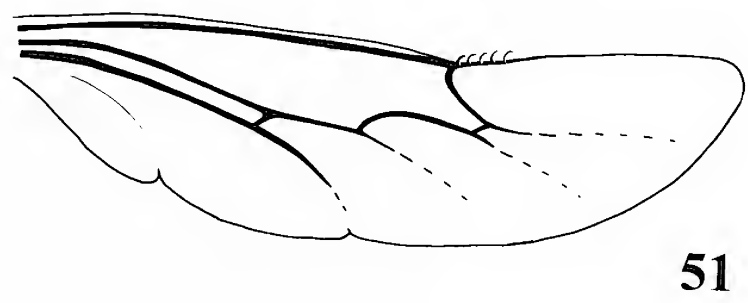


Fig. 49. Frontal view of head of holotype female of *Boreallodape baltica,* new species. Scale bar = 0.5 mm.

ETYMOLOGY: The new genus-group name is derived from *boreas* (Greek, meaning "north") and *Allodape,* type genus of the xylocopine tribe Allodapini. The name is a combined reference to the resemblance of species of this tribe to those of their sister tribe Allodapini and to the fact that these fossils are at the highest latitude recorded for any allodapine-like bee. The name is feminine.

COMMENTS: Species of *Boreallodape* su-





Figs. 50–51. Wings of holotype female of *Boreallodape baltica,* new species. **50.** Forewing. **51.** Hind wing. Scale bar = 0.5 mm.

perficially resemble the living allodapine genus *Braunsapis* but can be immediately separated from the latter (as well as all other Allodapini) by the tribal characteristics.

Key to Species of *Boreallodape*

1. Pleura strongly punctate, punctures well-defined, small and separated by a puncture width or less; tergal punctation closely spaced, separated by a puncture width at most; basal area of propodeum variable; larger species (body length more than 4 mm) 2
– Pleura impunctate; tergal punctation minute and sparse, puncture separated by 1–3 times a puncture width; basal area of propodeum glabrous; smaller species (body length less than 4 mm) . . . . . *B. mollyae,* n. sp.
2. Lower half of hypoepimeral area impunctate; punctures of mesepisternum not nearly contiguous, separated by 1–1.5 times a puncture width of smooth integument . . . . . *B. baltica,* n. sp.
– Hypoepimeral area uniformly punctured; punctures of mesepisternum nearly contiguous, when separated, then separated by less than a puncture width . . . . . *B. striebichi,* n. sp.

***Boreallodape baltica*, new species**

Figures 48–52

Plates 4a,b, 5b

Diagnosis: This species is most similar to *B. striebichi* but can be distinguished by the glabrous basal area of the propodeum, the more well-spaced pleural punctures (separated by smooth integument), and the presence

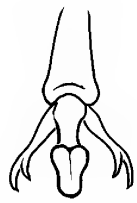


Fig. 52. Claw and arolium of holotype female of *Boreallodape baltica,* new species. Scale bar = 0.25 mm.

of a distinct impunctate region on the hypoepimeral area.

DESCRIPTION: **Female.** Total body length 4.47 mm; forewing length 2.56 mm. Head wider than long (length 1.03 mm, width 1.20 mm). Upper interorbital distance 0.75 mm; lower interorbital distance 0.60 mm. Interocellar distance 0.22 mm; ocellocular distance 0.17 mm; median ocellus to lateral ocellus 0.08 mm. Intertegular distance 0.80 mm. Basal vein distad cu-a by two times vein width; second abscissa Rs basad 1m-cu by four times vein width; 2rs-m relatively straight, distad 2m-cu by two times vein width; first submarginal cell longer than second submarginal cell.

Labrum with small punctures separated by 2–4 times a puncture width, integument between smooth. Clypeus with exceedingly faint, small punctures sparsely scattered. Supraclypeal area sculptured as on clypeus. Remainder of face with sparse, small punctures, integument between smooth, punctures become more closely packed (separated by two times a puncture width) toward upper part of face and vertex, integument between smooth; small impunctate zone lateral to and bordering lateral ocellus, impunctate zone less than 1OD in width and length. Gena with small punctures separated by 1–2 times a puncture width, integument between smooth; postgena sculptured as on gena. Pronotum with small punctures separated by 1–2 times a puncture width, integument between smooth. Mesoscutum with small punctures separated by a puncture width. Tegula with small, faint punctures on inner two-thirds, punctures separated by 1–2 times a puncture width. Scutellum with small punctures separated by 2–3 times a puncture width, integument between smooth. Metanotum with minute punctures separated by a puncture width or less, integument between smooth. Pleura strongly punctured, punctures approximately twice the diameter of those on mesoscutum, punctures separated by 1–1.5 times a puncture width except lower half of hypoepimeral area impunctate, integument between smooth. Metepisternum sculptured like mesepisternum except punctures separated by a puncture width or less and slightly smaller. Basal area of propodeum, metapostnotum, and posterior surface of propodeum impunctate and smooth; lateral surface of propodeum with small punctures separated by a puncture width, integument between smooth. First metasomal tergum impunctate; T2 with coarse, faint punctures separated by a puncture width or less except central disc impunctate and punctures bordering this area more widely separated and more faint; remaining terga with coarse, faint punctures separated by a puncture width or less, without impunctate zone on central discs.

Integumental coloration not preserved. Wing membrane hyaline; veins strong and dark brown.

Setae simple, minute or short, and sparse except those of sterna erect, short and more dense.

MATERIAL: Eight specimens. **Holotype.** Female, B-JH 152 (AMNH) labeled "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Boreallodape baltica* Engel". **Paratype.** Female, Nr. 1–5: 1967 (ZMUC) labeled: "Apidae, C. V. Henningsen, 1–5, 1967" // "Paratype, *Boreallodape striebichi* Engel". This specimen is missing the very apex of the head (right mandible, lateral two-thirds of labrum, apex of right compound eye, and lateral third of clypeus), which is right at the surface of the amber. There are also some thin layers of Schimmel on the bee.

Paratype. Female, Nr. 810 (CDTG) labeled: "Nr. 810" // "Paratype, *Boreallodape baltica* Engel".

Paratype. Female, Nr. 873 (CHFG) labeled: "Nr. 873, Balt. Bernstein" // "Paratype, *Boreallodape baltica* Engel".

Fig. 53. Dorsal view of holotype female of *Boreallodape mollyae,* new species.

Paratype. Female, Nr. 1253 (CHFG) labeled: "Nr. 1253, Balt. Bernstein" // "Paratype, *Boreallodape baltica* Engel".

Paratype. Female, Nr. 1256 (CHFG) labeled: "Nr. 1256, Balt. Bernstein" // "Paratype, *Boreallodape baltica* Engel".

Paratype. Female, Nr. 70 (CJDL) labeled: "Nr. 70" // "Paratype, *Boreallodape baltica* Engel".

Non-type. Female, B-W 159 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Boreallodape baltica*? Engel, det. M. S. Engel".

ETYMOLOGY: The specific epithet is a reference to the Baltic region where the amber originates.

Boreallodape mollyae, new species

Figures 53, 54

Plates 4e, 5a

DIAGNOSIS: This is the smallest species of the genus. *Boreallodape mollyae* can be recognized by the combination of impunctate pleural integument (unique for the genus) and minute and relatively sparse metasomal punctation.

DESCRIPTION: **Female.** Total body length 3.68 mm; forewing length 2.34 mm. Head wider than long (length 0.97 mm, width 1.13 mm). Upper interorbital distance 0.65 mm; lower interorbital distance 0.50 mm. Interocellar distance 0.18 mm; ocellocular distance 0.17 mm; median ocellus to lateral ocellus 0.08 mm. Intertegular distance 0.77 mm. Basal vein distad cu-a by two times vein width; second abscissa Rs basad 1m-cu by four times vein width; 2rs-m relatively straight, distad 2m-cu by two times vein width; first submarginal cell longer than second submarginal cell.

Labrum with small punctures separated by 1–3 times a puncture width, integument between smooth. Clypeus with small punctures separated by 2–3 times a puncture width. Supraclypeal area sculptured as on clypeus. Remainder of face with sparse, small punctures, integument between smooth, punctures becoming gradually more closely spaced again (separated by 2–4 times a puncture width) on upper part of face and vertex, integument between smooth. Gena with minute punctures separated by 3–4 times a puncture width, integument between smooth; postgena with small punctures separated by 1–2 times a puncture width, integument between smooth. Pronotum impunctate, faintly imbricate. Mesoscutum with small punctures separated by

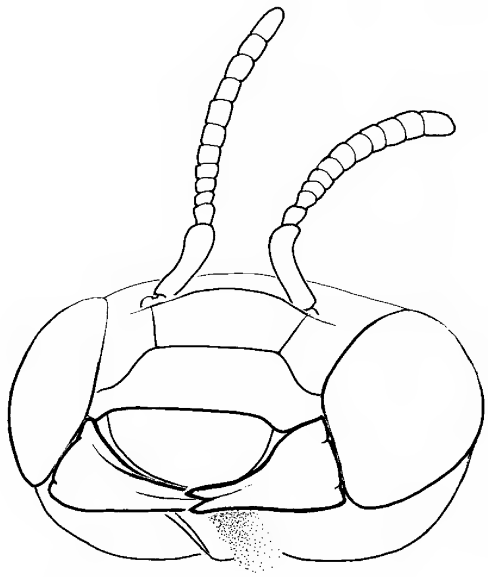


Fig. 54. Frontoventral oblique view of head of holotype female of *Boreallodape mollyae,* new species. Scale bar = 0.5 mm.

a puncture width, integument between smooth. Tegula with minute punctures, punctures separated by 1–2 times a puncture width. Scutellum sculptured as on mesoscutum. Metanotum with minute punctures separated by 2–3 times a puncture width, integument between smooth. Mesepisternum impunctate and smooth except for a few exceedingly faint punctures sparsely scattered, hypoepimeral area impunctate. Metepisternum impunctate. Propodeum impunctate and smooth. T1–T2 impunctate; T3–T5 with minute punctures separated by 2–3 times a puncture width, integument between smooth; T6 with minute punctures separated by 1–2 times a puncture width, integument between smooth; sterna imbricate.

Where preserved (mesoscutum, scutellum, metasoma) integument dark brown and shining with reddish-brown highlights. Wing membrane hyaline; veins dark brown.

Setae simple, minute or short, and sparse except those of sterna erect, short and more dense.

MATERIAL: Six specimens. **Holotype.** Female, B-JH 81 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Boreallodape mollyae* Engel".

Paratypes. Five females, Nr. 19948 (ZMPA) labeled: "Muzeum Ziemi w Warszawie, 19948, Baltic amber with bees, Apidae, from Baltic beach in Stupsk, 1983" // "Baltic Amber: Eocene, Nr. 19948, Muzeum Ziemi Pan, M. S. Engel study" // "Paratype, *Boreallodape mollyae* Engel".

ETYMOLOGY: The specific epithet is a patronymic in loving honor of Ms. Molly G. Rightmyer, brilliant hymenopterist and gifted artist, who executed the numerous magnificent illustrations presented herein.

Boreallodape striebichi, new species

Figures 55–58

Plate 4c,d,f

DIAGNOSIS: This species is most similar to the type species for the genus, *B. baltica,* but differs in the punctation of the pleura and sculpturing of the propodeum (refer to Diagnosis for *B. baltica*).

DESCRIPTION: **Female.** Total body length 4.54 mm; forewing length 2.91 mm. Head wider than long (length 1.13 mm, width 1.34 mm). Upper interorbital distance 0.84 mm; lower interorbital distance 0.63 mm. Interocellar distance 0.28 mm; ocellocular distance 0.22 mm; median ocellus to lateral ocellus 0.13 mm. Intertegular distance 0.97 mm. Basal vein distad cu-a by two times vein width; second abscissa Rs basad 1m-cu by four times vein width; 2rs-m relatively straight, distad 2m-cu by two times vein width; first submarginal cell longer than second submarginal cell.

Labrum with small punctures separated by 2–4 times a puncture width, integument between smooth. Clypeus with faint, small punctures sparsely separated by 1–3 times a puncture width. Supraclypeal area and face sculptured as on clypeus; punctures becoming more closely packed (separated by less than a puncture width) toward upper part of face and vertex, integument between smooth; small impunctate zone lateral to and bordering lateral ocellus, impunctate zone less than 1OD in width and length. Gena with small punctures separated by less than a puncture width, integument between finely imbricate; postgena

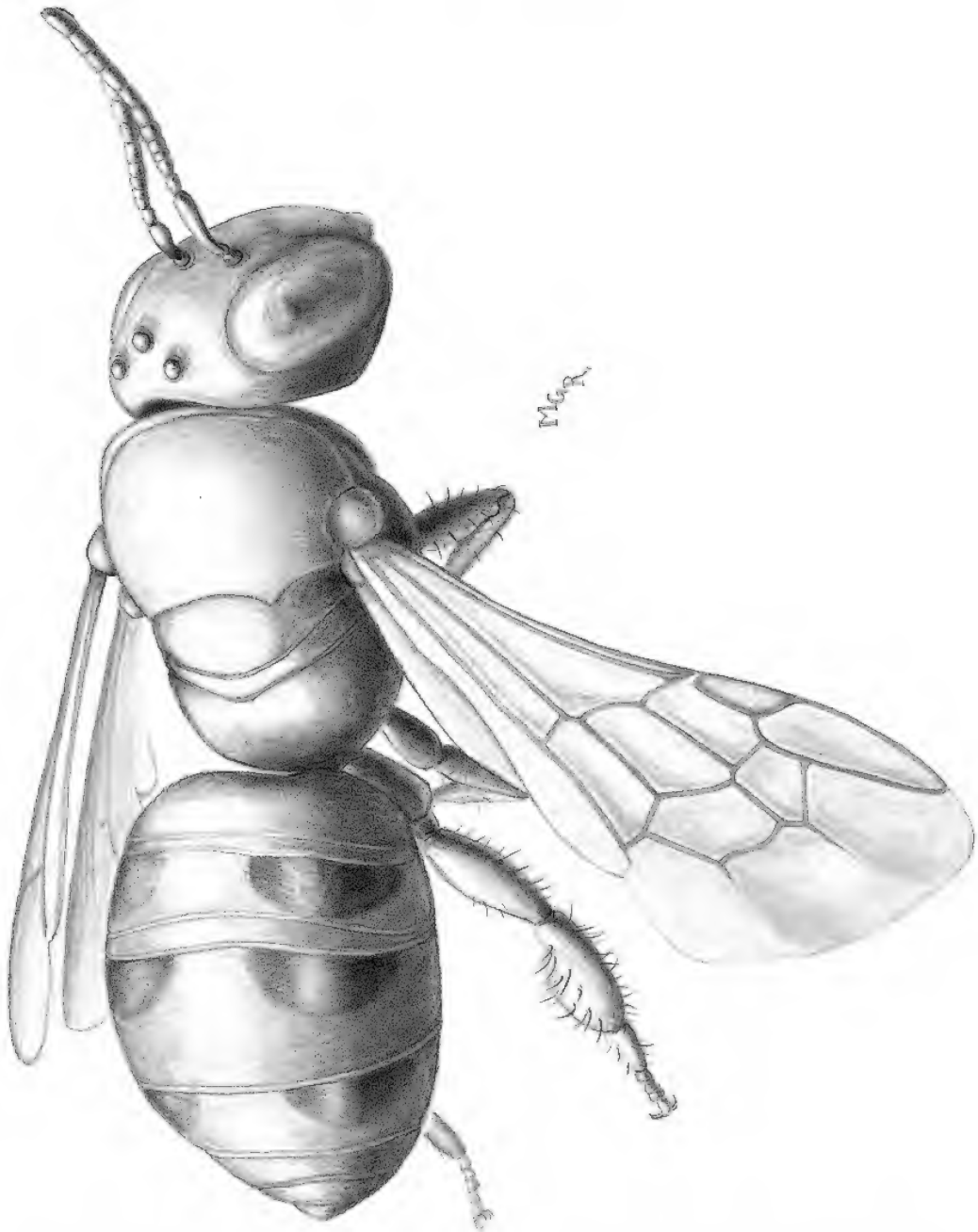


Fig. 55. Right dorsolateral habitus of holotype female of *Boreallodape striebichi,* new species.

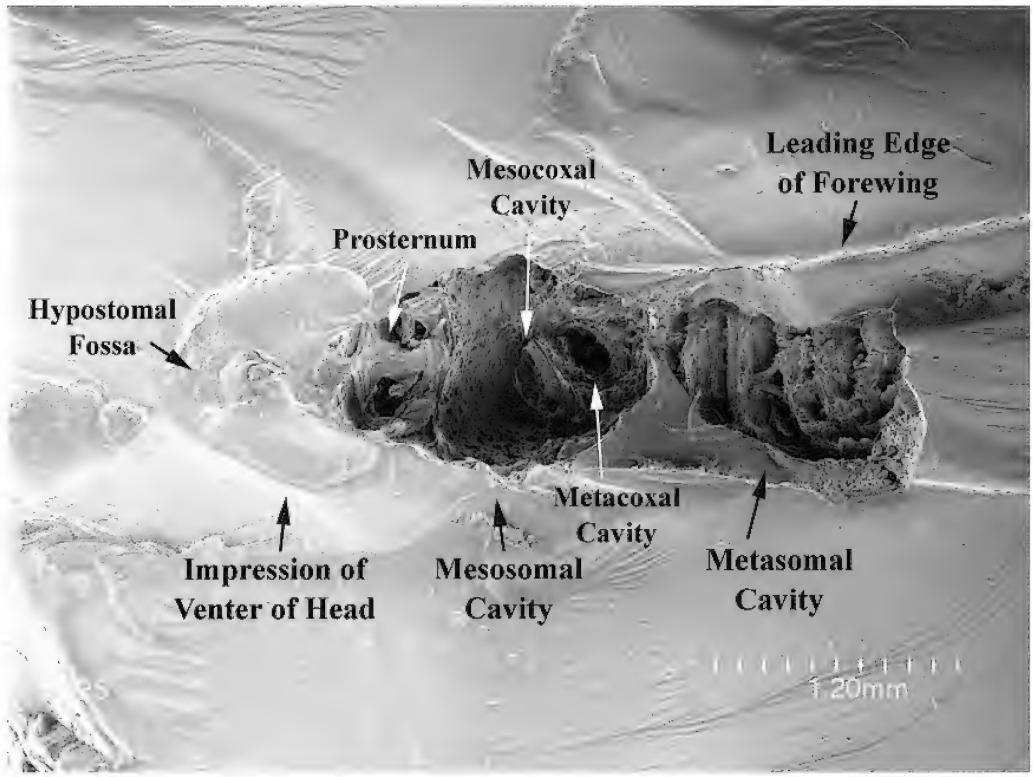


Fig. 56. Scanning electron micrograph of paratype female of *Boreallodape striebichi,* new species; partial specimen preserved at amber surface of B-BS 153 (AMNH).

sculptured as on gena. Pronotum with small punctures separated by a puncture width or less, integument between finely imbricate. Mesoscutum with small punctures separated by a puncture width, integument between smooth. Tegula with minute, faint punctures on inner two-thirds, punctures separated by two times a puncture width. Scutellum sculptured as on mesoscutum. Metanotum with minute punctures separated by a puncture width or less, integument between smooth. Pleura strongly punctured, punctures separated by less than a puncture width or more often contiguous, hypoepimeral area without impunctate zone, integument between (where evident) smooth. Metepisternum sculptured as on mesepisternum. Basal area of propodeum, metapostnotum, and posterior surface of propodeum imbricate; lateral surface of propodeum with small punctures separated by less than a puncture width, integument between faintly imbricate. First metasomal tergum impunctate; T2 with coarse, faint punctures separated by a puncture width or less except punctures of central disc more widely separated and faint, without impunctate area; remaining terga with coarse, faint punctures separated by a puncture width or less.

Integumental coloration dark brown where preserved. On some individuals yellow markings are easily apparent along the inner margin of the compound eyes below the level of the anterior tentorial pits as well as small areas on the lateral apical borders of the clypeus. Wing membrane hyaline; veins dark brown.

Setae simple, minute or short, and sparse except those of sterna erect, short, and more dense.

MATERIAL: Fourteen specimens. **Holotype.** Female (pl. 4c, 4d), B-BS 153 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad,

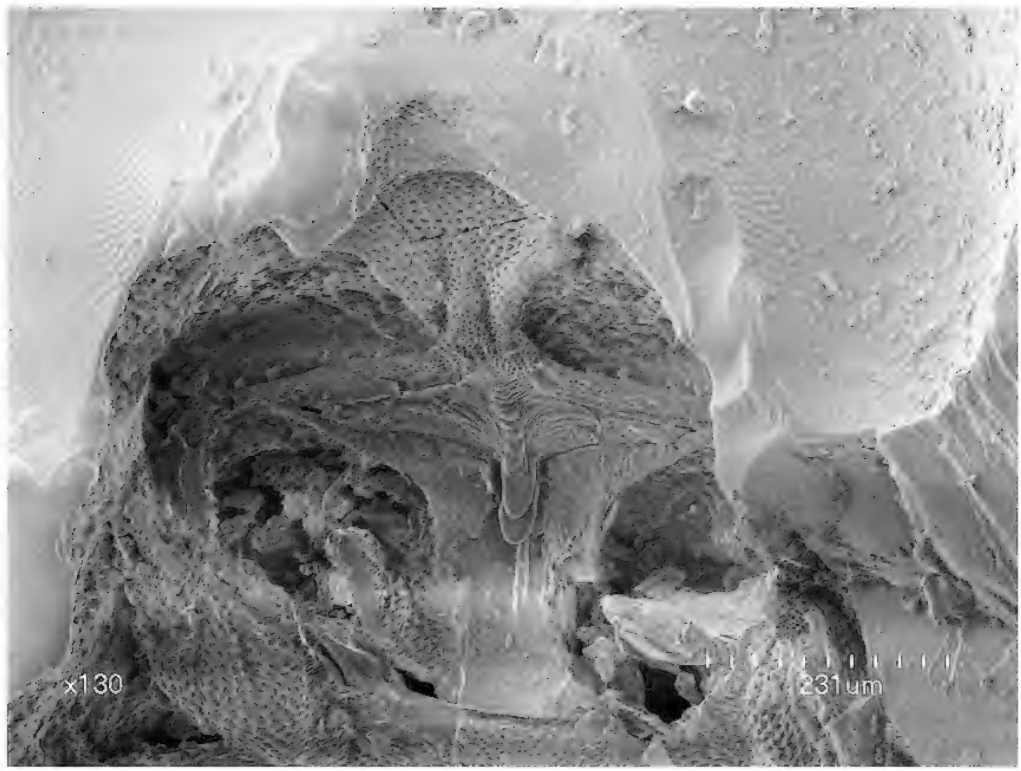


Fig. 57. Scanning electron micrograph of paratype female of *Boreallodape striebichi,* new species. Magnified view of prosternum from figure 56.

Yantarny" // "Holotype, *Boreallodape striebichi* Engel". There are several specimens in this single piece (designated as paratypes below). The holotype is the single individual depicted in plate 4c, 4d. There is some pyrrhite on the specimen (e.g., on supraclypeal area) that makes the sculpturing difficult to interpret in some areas.

Paratypes. Eight whole females and five partial females, B-BS 153 (AMNH): in the same block of amber as the holotype.

ETYMOLOGY: The specific epithet is a patronymic honoring Herr Bernhard Striebich, Buxtehude (Germany), who generously donated the holotype and its associated paratypes to the AMNH.

COMMENTS: The shape of the clypeus in this species appears to be slightly different from that of other *Boreallodape.* The lateral margins of the clypeus are not as strongly concave and the portion of the clypeus above the bend in the lateral margins and above the anterior tentorial pits is shorter (thereby the supraclypeal area is correspondingly longer than in the other species). Thus, the clypeus is more plesiomorphic (more closely approximating that shape seen in Manueliini) than other *Boreallodape* species. I presently interpret this species as the basalmost species of *Boreallodape.*

Boreallodape sp. indet.

MATERIAL: One specimen. **Non-type.** Female, B-W 163 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Boreallodape* sp. indet., det. M. S. Engel."

COMMENTS: This specimen is mostly covered by debris, and although the wing venation, metasoma, and legs can be examined easily, the remainder of the body cannot be seen clearly.

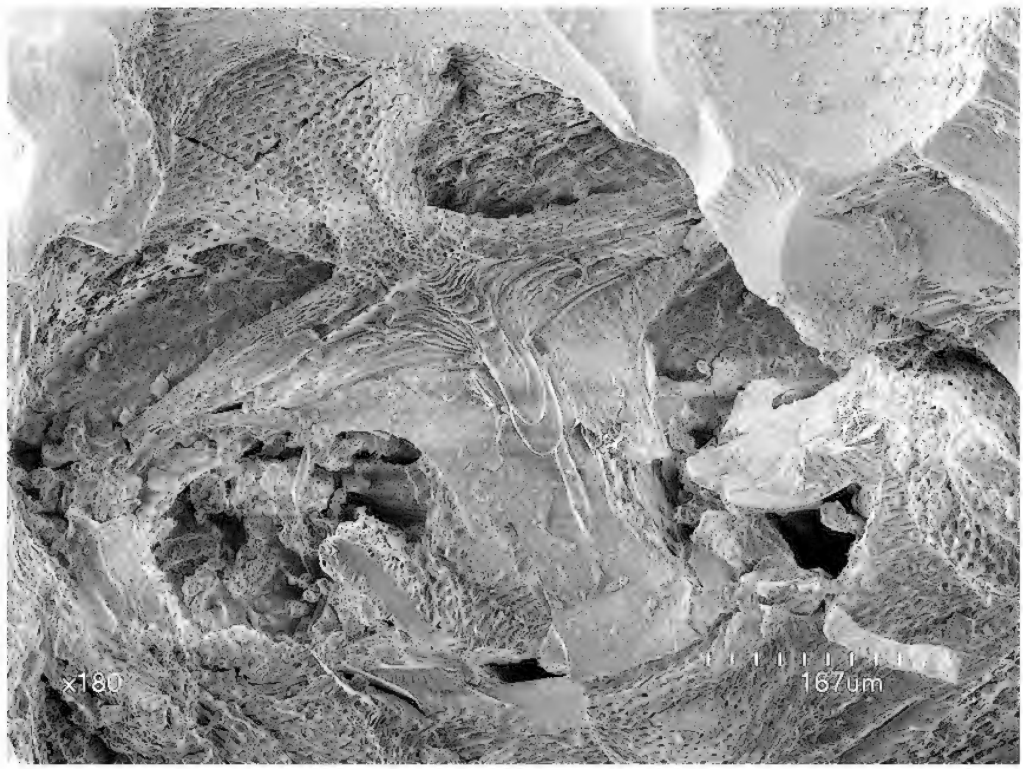


Fig. 58. Scanning electron micrograph of paratype female of *Boreallodape striebichi,* new species. Magnified and slightly oblique view of prosternum.

Subfamily Apinae Latreille "Corbiculate Apinae"

Apiariae Latreille, 1802a: 373. Type genus: *Apis* Linnaeus, 1758.

Diagnosis: The corbiculate apines, as the name implies, can be immediately recognized by the modification of the metatibia into a corbicula in nonparasitic females and workers. The presence of a rastellum, an expanded mandibular pollex, as well as the absence of the metabasitibial plate and pygidial plate also serve to distinguish this clade from other apines as well as the Xylocopinae (the only other subfamily of Apidae presently known in Baltic amber). At present, only the corbiculate tribes of Apinae are known from Baltic amber.

Description: Mandibular pollex expanded. Metatibia modified into corbicula; metabasitibial plate absent; inner apical margin of metatibia with rastellum; auricle frequently present (except in parasitic forms and Meliponini). Wings uniformly setose. Prepygidial fimbria and pygidial plate absent.

Comments: The name "corbiculate bees", or Corbiculata, was first coined by Shuckard (1866: 165) for this specialized group of apine bees. This distinctive clade was once considered as the family Apidae (e.g., Michener, 1965, 1990) with the other apids relegated to the paraphyletic family Anthophoridae. The recent study of long-tongued bee phylogeny by Roig-Alsina and Michener (1993) resurrected the expanded concept of Apidae as it was employed by Michener (1944) and the corbiculate bees were incorporated into an expanded subfamily Apinae without a separate, formal rank. Should a formal rank be useful for recognizing the corbiculate apines, the supertribal name Apiti could be applied. Presently, an apine clade

containing the non-corbiculate tribes Anthophorini, Centridini, Melectini, and Ericrocidini[6] is believed to be the closest relative of the corbiculate Apinae (refer to fig. 123).

This is the most common group of bees in Baltic amber. Three of the living tribes are eusocial to varying degrees and the phylogenetic position of the extinct corbiculate groups suggests that they too were eusocial (refer to sections on Cladistic Analyses, below). This social lifestyle perhaps can account for their abundance in amber in comparison to other groups. Living corbiculate bees typically collect resins and it is possible that the fossil species described below did as well, thus subjecting them more frequently to entrapment and fossilization.

The corbiculate clade consists of four extant tribes, briefly summarized as follows: The Apini (honey bees) are originally an Old World group but have been spread throughout the world by humans for agricultural purposes. Presently, fossils of Apini are only known from as far back as the early Oligocene (Engel, 1998c, 1999c). The Euglossini (orchid bees) are strictly neotropical with two species in Miocene amber from the Dominican Republic (Engel, 1999b) and one extant species occurring in South American copal (Engel, personal obs.; Ross, 1998). The bumble bees, tribe Bombini, are distributed throughout the western hemisphere, the Palearctic, and the Oriental regions. The report of a bumble bee from tropical Africa (Tkalců, 1966) is actually based upon on an introduced species from South America (Sakagami, 1976; Michener, 1979, 1990; Williams, 1998). Numerous fossil bumble bees are known [Heer, 1867; Unger, 1867; Novak, 1877; Cockerell, 1906 (as *Calyptapis*), 1931; Piton, 1940 (as *Probombus*); Zhang, 1990; Zhang et al., 1994; Rasnitsyn and Michener, 1991; Riou, 1999] but no true bombine has yet been discovered in amber. The report of a bombine in Paleocene amber from France (*In* Grimaldi, 1999) has yet to be confirmed; it is possible that this fossil is an electrobombine (if a small jugal lobe is present in the hind wing). Lastly, the stingless bees, tribe Meliponini, are diverse pantropically. Species are known in Late Cretaceous New Jersey amber (Michener and Grimaldi, 1988a, 1988b; Engel, 2000b), Miocene Dominican amber (Wille and Chandler, 1964; Michener, 1982; Camargo et al., 2000), Oligocene-Miocene Mexican amber (Wille, 1959), Colombian copal (Engel, personal obs.), Burmese copal [Cockerell, 1921 (not Miocene amber!)], Sicilian amber [Tosi, 1896 (perhaps copal?)], and African copal [Engel, personal obs.; Stuckenberg, 1975 (not Baltic amber!); Zeuner and Manning, 1976; Wille, 1977]. Of all of these Recent tribes, only the meliponines are presently known in Baltic amber.

[6] Despite that shown in figure 123, relationships among these four non-corbiculate tribes are somewhat uncertain and nodes are not strongly supported. It is very likely that, once resolved, Anthophorini and Melectini will be sister groups and together sister to a monophyletic Centridini + Ericrocidini clade.

Key to Tribes of Corbiculate Apinae in Baltic Amber

1. Distal wing venation complete (e.g., figs. 62, 68, 75, 77); marginal cell closed at apex; metatibial spurs present (fig. 71); auricle present (e.g., figs. 81, 90, 106); supra-alar carina present; claws with inner tooth (e.g., figs. 61, 108) 2
– Distal wing venation incomplete (figs. 111, 113); marginal cell open at apex; metatibial spurs absent; auricle absent (fig. 114; supra-alar carina absent; claws simple (fig. 115) .... Meliponini Lepeletier de Saint Fargeau
2. Outer grooves of mandible present; hamuli not reduced, 10 or more (fig. 63); 1m-cu not strongly angulate (e.g., figs. 62, 66); one or two metatibial spurs present; robust, *Bombus*- or *Apis*-like bees 3
– Outer grooves of mandible absent; hamuli reduced in number, less than 10 (figs. 92, 104, 110); 1m-cu short and strongly angulate (figs. 91, 103, 109); single metatibial spur present (figs. 90, 102, 107); frequently small, *Trigona*-like bees .... Melikertini, n. tribe
3. Alar papillae absent (figs. 66–68, 73–77, 85); outer mandibular grooves reduced but present; one metatibial spur present (figs. 71, 83); marginal cell either weakly truncate or appendiculate ..... Electrapini Engel
– Alar papillae present (figs. 62, 63); outer mandibular grooves present and strong; two metatibial spurs present; marginal cell narrowly rounded at apex, not truncate or appendiculate ... Electrobombini, n. tribe

ELECTROBOMBINI, New Tribe

TYPE GENUS: *Electrobombus* Engel, new genus.

DIAGNOSIS: Robust *Bombus*-like bees that resemble in almost every respect the tribe Bombini; however, the presence of a distinct jugal lobe at the base of the hind wing, a well-developed pterostigma that is much larger than the prestigma, and a strongly developed arolium serve to distinguish the electrobombines from bombines. Electrobombini can be separated from primitive Electrapini by the presence of strongly developed outer mandibular grooves and two elongate metatibial spurs.

DESCRIPTION: Large (ca. 18 mm long), robust, densely pubescent bees. Mandible with strong outer mandibular grooves present. Labral width two times length (fig. 59). Clypeus slightly convex and weakly protuberant in lateral view. Compound eyes bare. Supraälar carina present; scutellum broadly rounded posteriorly and projecting over metanotum and (perhaps?) propodeum. Claws of female with inner tooth; arolium present and strong (fig. 61); two metatibial spurs present; malus of strigilis with short anterior velum in addition to primary ventral velum; metabasitarsus with distinct auricle at base (fig. 60); metatibia without penicillum (fig. 60). Distal venation of forewing strong and present; marginal cell large and narrowly rounded at apex, slightly offset from wing margin, not truncate or appendiculate, cell longer than distance from its apex to wing apex (fig. 62); pterostigma present and moderately sized, much longer than prestigma, r-rs arising slightly prior to its midpoint, margin within marginal cell straight; 1m-cu relatively straight; hind wing with small but distinct jugal lobe, lobe broadly incised (fig. 63); hamuli numerous (15 in a single series for *Electrobombus samlandensis*); wing membrane papillate in outer margins (figs. 62, 63). Sting not reduced, not barbed.

Electrobombus, new genus

TYPE SPECIES: *Electrobombus samlandensis* Engel, new species.

DIAGNOSIS: As for the tribe (see above).

DESCRIPTION: Mandible with a few weak apical teeth. Malar space short, shorter than basal mandibular width. Epistomal sulcus forming obtuse angle (fig. 59). Inner margins of compound eyes slightly converging below, not emarginate. F1 longer than F2–3 combined; F3 longer than F2. Preoccipital ridge rounded. Mesoscutal anterior border broadly rounded; scutellum projecting over metanotum and basal area of propodeum. Basal area of propodeum apparently strongly declivitous. Keirotrichiate field not elevated; metatibial spurs serrate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae; metabasitarsus twice as long as wide. Margin of pterostigma within marginal cell straight; marginal cell apex offset from wing margin by slightly less than pterostigma width, apex rounded, not appendiculate.

ETYMOLOGY: The new genus-group name is a combination of *elektron* (Greek, meaning "amber") and the generic name *Bombus* (originally taken from the Greek *bombos,* meaning "buzzing", which itself is related to *bombylios,* meaning "bumble bee").

Electrobombus samlandensis, new species

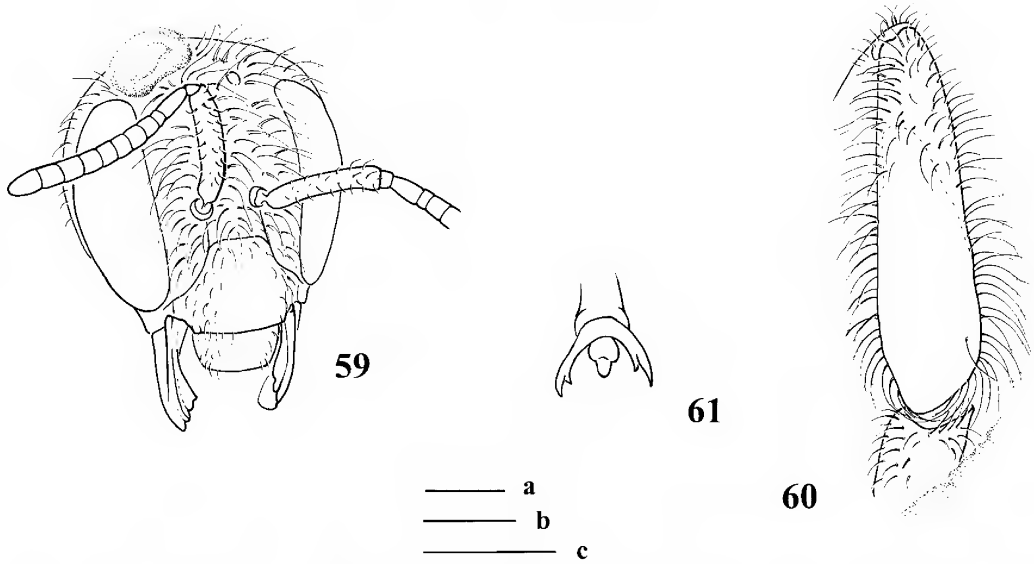
Figures 59–63

Plate 5c, e

DIAGNOSIS: As for the genus.

DESCRIPTION: **Female.** Total body length 18.78 mm; forewing length 10.50 mm. Head longer than wide (length 3.40 mm, width 3.24 mm). Upper interorbital distance 1.50 mm; lower interorbital distance 1.45 mm. Interocellar distance indeterminate (owing to bubble that obscures the position of one lateral ocellus); ocellocular distance 0.35 mm; median to lateral ocellus 0.20 mm. Intertegular distance 3.75 mm. Basal vein basad cu-a by three times vein width; 1rs-m distad by 1m-cu by seven times vein width; 2rs-m distad 2m-cu by vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-half that of posterior border; length of anterior border of third submarginal cell one-half of that of posterior border, 1.5 times length of anterior border of second submarginal cell; 15 hamuli, arranged in a single, evenly spaced series.

Integument, where visible between dense pubescence of head, mesosoma, and meta-



Figs. 59–61. Holotype female of *Electrobombus samlandensis,* new species. **59.** Oblique frontal view of head. **60.** Outer surface of metatibia and basal portion of metabasitarsus. **61.** Claw and arolium. Scale bars = 1 mm (a = fig. 60; b = fig. 59; c = fig. 61).

soma, smooth and impunctate except face, clypeus, and supraclypeal area with small, faint punctures separated by a puncture width or less, tegula with microscopic punctures separated by 2–3 times a puncture width, and terga and sterna imbricate.

Coloration of head and mesosoma black; metasoma, antennae, and legs dark brown. Wing membrane hyaline; veins strong and dark brown.

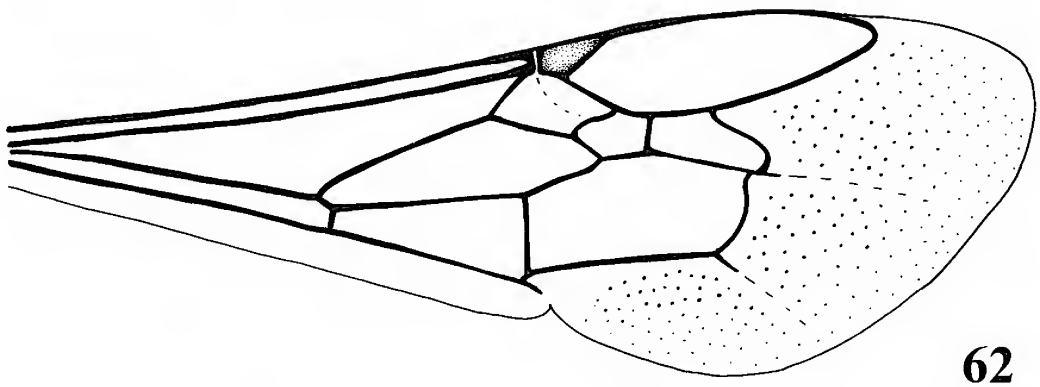
Pubescence generally yellowish-white. Mandible with dense, minute setae in apical halves of outer grooves. Labrum with widely scattered, short, simple, erect setae. Clypeus with scattered, erect setae, such setae slightly more numerous along lateral borders. Face with dense, short, appressed, plumose setae mostly obscuring integument intermixed with longer, erect to suberect, plumose setae. Vertex with long, plumose, erect setae. Gena with pubescence as described for vertex except setae with only a few, minute branches. Mesosomal (dorsal, lateral, and ventral) pubescence long, feathery plumose, and exceedingly dense, mostly obscuring integument. Tegula with rather sparse, short, appressed setae not obscuring integument. Long corbicular setae with numerous, minute branches intermixed with long, simple setae. Terga and sterna with minutely branched, dense, moderate-length, subappressed setae that partly obscure the integument.

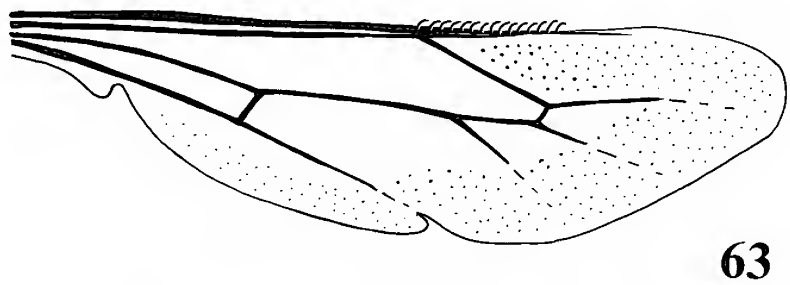
MATERIAL: Two specimens. **Holotype.** Female (caste indeterminate), B-JH 94 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Electrobombus samlandensis* Engel".

Non-type. Female (caste indeterminate), Nr. 500 (CJDL) labeled: "Nr. 500" // "*Electrobombus samlandensis*?, det. M. S. Engel". This individual is entirely covered in Schimmel. Those few characters that can be determined suggest that the specimen is a second individual of *E. samlandensis* but this will perhaps never be known with certainty. The specimen is even larger than the holotype and is the largest bee specimen known from Baltic amber (total body length 22 mm).

ETYMOLOGY: The specific epithet is a reference to the Samland Peninsula where most Baltic amber has been uncovered.

COMMENTS: This is presently the largest





Figs. 62–63. Wings of holotype female of *Electrobombus samlandensis,* new species. **62.** Forewing. **63.** Hind wing. Scale bar = 1 mm.

bee species preserved in amber (of any deposit!).

Tribe Electrapini Engel, Nomen Translatum

Electrapina Engel 1998a: 99. Type genus: *Electrapis* Cockerell, 1908b.

Diagnosis: The electrapine bees are a heterogeneous group of three genera resembling either bumble bees (Bombini) or, to a much lesser degree, honey bees (Apini). From the former tribe electrapines differ by the presence of a jugal lobe, absence of alar papillae, truncated or appendiculate marginal cell apex, reduction of the outer mandibular grooves, and presence of only one, reduced metatibial spur. From the Apini, the electrapines differ by the deep incision demarking the jugal lobe, the presence of outer mandibular grooves, the single metatibial spur (entirely absent in Apini), the absence of long eye setae (some microscopic setae are present in many specimens as is typical for many bees), and the shape of the marginal and submarginal cells in the forewing, among other characters.

Description: Moderately sized (ca. 5.5–16 mm long), robust, densely pubescent bees. Mandible with weakened outer mandibular grooves. Labral width 2–3 times length. Clypeus slightly convex and weakly protuberant in lateral view or flat (in *Thaumastobombus*). Compound eyes bare or with sparse, microscopic setae. Supraälar carina present; scutellum broadly rounded posteriorly and variously produced (ranging from projecting over metanotum and propodeum

to over metanotum only). Claws of female with inner tooth (e.g., figs. 72, 83); arolium strong and present; single, reduced metatibial spur present; malus of strigilis with short, thickened anterior prong in addition to primary ventral velum (e.g., fig. 82); metabasitarsus with distinct auricle at base; metatibia without penicillum. Distal venation of forewing strong and present; marginal cell large and narrowly rounded at apex, slightly offset from wing margin, truncate or feebly appendiculate, cell longer than distance from its apex to wing apex; pterostigma present and short to moderately sized, much longer than prestigma, r-rs arising near to just after midpoint, margin within marginal cell variously produced; 1m-cu relatively straight; hind wing with distinct jugal lobe, lobe broadly and deeply incised; hamuli numerous or reduced (numerous in *Electrapis* and *Protobombus,* reduced in *Thaumastobombus*); wing membrane without alar papillae. Sting not reduced; with or without microscopic barbs.

COMMENTS: There has been much confusion over the identity of *Electrapis* and its tribal position among the corbiculate bees. Recently I erected the Electrapina as a subtribe of Apini to accommodate the nominate genus as it had been conceived by more recent authors (e.g., Zeuner and Manning, 1976; Kelner-Pillault, 1970a; Engel, 1998a) but my recent revelations over the true identity and nature of the type species (see below in Comments under *Electrapis* and *E. meliponoides*) have resulted in a radical reinterpretation of the group. Those bees believed to be *Electrapis* s.l. in recent decades, and thereby somewhat intermediate in character between Apini and Meliponini are, in fact, members of the Melikertini (treated below). The electrapines are, in fact, intermediate in some respects between bombines and the Apini + Meliponini clade (see Cladistic Analyses, below). Cockerell's (1908b, 1909b, 1909c) notes on the genus, as well as the genus *Protobombus,* clearly indicate overall *Bombus*-like bees (although some have a definite *Apis*-like habitus) and provide the necessary characters to associate his species with the specimens described below as *Electrapis* and *Protobombus.* Other taxa (i.e., those thought to resemble meliponines) at one time placed in or near *Electrapis* by Kelner-Pillault (1970a), Manning (1960), Zeuner and Manning (1976), as well as myself (Engel, 1998a), are reassigned to the Melikertini or in a few instances to other electrapine genera following the results of the cladistic analysis presented below.

TABLE 8
Hierarchical Classification of Tribe †Electrapini

†TRIBE ELECTRAPINI ENGEL
- Genus *Electrapis* Cockerell
  - *Electrapis meliponoides* (Buttel-Reepen)
  - *Electrapis tornquisti* Cockerell
  - *Electrapis krishnorum* Engel
  - *Electrapis martialis* (Cockerell)
  - *Electrapis electrapoides* (Lutz)[a]
- Genus *Protobombus* Cockerell
  - *Protobombus indecisus* Cockerell
  - *Protobombus tristellus* Cockerell
  - *Protobombus hirsutus* (Cockerell)
  - *Protobombus fatalis* (Cockerell)
  - *Protobombus basilaris* Engel
- Genus *Thaumastobombus* Engel
  - *Thaumastobombus andreniformis* Engel

[a]Compression fossil from the middle Eocene of Germany (not treated further herein).

The tribe Electrapini, even after the removal of *Melikertes* and *Roussyana,* may still be paraphyletic with respect to an Apini + Meliponini + Melikertini clade. Among the three genera of electrapines known, *Electrapis* is the most plesiomorphic and resembles not only *Electrobombus* (from which it differs most significantly by the tribal characters mentioned above) but living bombines as well. *Protobombus* appears somewhat intermediate between *Electrapis* and *Thaumastobombus,* the latter appearing most similar to the higher corbiculates (i.e., Apini, Meliponini, and Melikertini). However, there is presently not enough cladistic information to resolve the issue, and this scheme is presented only as a working hypothesis upon which future studies can build. It is appropriate to pose the possibility that electrapines may represent a stem-group lineage from which the higher corbiculates originated. Table 8 summarizes the present classification of Electrapini.

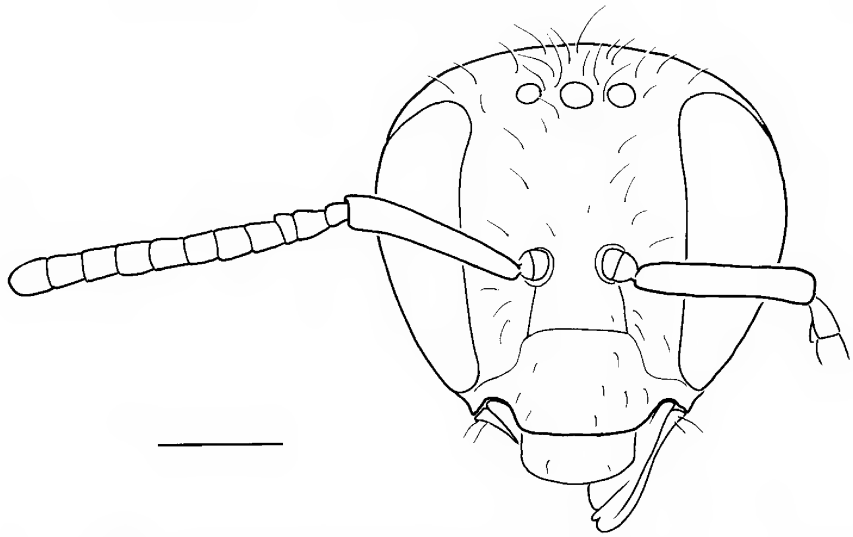


Fig. 64. Frontal view of head of female *Electrapis martialis* (Cockerell). Scale bar = 1 mm.

Key to Genera of Electrapini

1. Metabasitarsus elongate, 1.5–2 times as long as maximum width (fig. 65) . . . . . *Electrapis* Cockerell
– Metabasitarsus quadrangular, as long as maximal width (figs. 70, 78, 81) 2
2. Lateral margins of clypeus strongly concave, epistomal sulcus forming an obtuse angle opening toward compound eye (fig. 69) . . . . . *Protobombus* Cockerell
– Lateral margins of clypeus linear, epistomal sulcus straight (figs. 79, 80) . . . . . *Thaumastobombus,* n. gen.

Genus *Electrapis* Cockerell, revised status

Electrapis Cockerell, 1908b: 326. Type species: *Apis meliponoides* Buttel-Reepen, 1906, by designation of Cockerell, 1909b. Cockerell, 1909b: 7. Zeuner and Manning, 1976: 227.
Elektrapis Bischoff, 1927: 454. *Lapsus calami.*
Eckfeldapis Lutz, 1993: 180. Type species: *Eckfeldapis electrapoides* Lutz, 1993, monobasic and original designation.

DIAGNOSIS: This genus can be separated from other genera in the tribe by the angled epistomal sulcus (fig. 64) and elongate metabasitarsus (fig. 65).

DESCRIPTION: Mandible with a few, weak apical teeth. Malar space short, shorter than basal mandibular width (fig. 64). Epistomal sulcus forming orthogonal or obtuse angle (fig. 64). Inner margins of compound eyes slightly converging below, weakly emarginate. F1 longer than F2, not longer than combined lengths of F2 and F3; F3 longer than F2. Preoccipital ridge rounded. Prosternum without constriction between basisternum and furcasternum; similar in construction to *Bombus*; apophyseal pit present. Mesoscutal anterior border broadly rounded; scutellum projecting over metanotum and basal area of propodeum. Basal area of propodeum strongly declivitous. Keirotrichiate field not elevated; metatibial spur serrate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae; metabasitarsus 1.5–2 times as long as wide (fig. 65). Margin of pterostigma within marginal cell concave to convex; marginal cell apex offset from wing margin by pterostigma width or more, apex either rounded and appendiculate or truncate. Sting usually not barbed (except in some specimens of *Protobombus* and one of *Thaumastobombus* microscopic barbs are apparently present).

COMMENTS: One species of *Electrapis* has been discovered as a compression fossil in the middle Eocene oil-shale sediments of Eckfelder Maar Formation [*E. electrapoides*

(Lutz) (Lutz, 1993; Engel, 1998a: 101)]. With the splitting of *Electrapis* into multiple genera, *Eckfeldapis* remains a junior synonym of *Electrapis* s.s. (e.g., elongate metabasitarsus, identical wing venation). *Electrapis electrapoides* has not been included in the following key to species.

An individual of a species of *Electrapis* (GPUH Nr. 3001; see below) is preserved with its dorsum open at the amber surface thereby allowing examination of the prosternal structure. It is from this individual that the above definition of the *Electrapis* prosternal construction is based.

Key to Species of *Electrapis* in Baltic Amber

1. Pterostigma size normal, longer than wide (fig. 66) 2
– Pterostigma exceptionally short, length equal to width (fig. 68) .... *E. meliponoides* (Buttel-Reepen)
2. Labral apex without distinctive patches of elongate setae 3
– Labral apex with patches of elongate setae bordering midpoint .... *E. tornquisti* Cockerell
3. Apical margins of T2–5 with bands of dense, short, plumose setae; hind wing with first abscissa M 3.5–4.5 times length of rs-m; forewing 2rs-m distad 2m-cu by at least twice vein width ..... *E. martialis* (Cockerell)
– Apical margins of T2–5 without bands of dense, short, plumose setae; hind wing with first abscissa M 1.5–2 times length of rs-m (fig. 67); forewing 2rs-m confluent with 2m-cu ..... *E. krishnorum,* n. sp.

Electrapis martialis (Cockerell), new combination

Figure 64

Chalcobombus martialis Cockerell, 1908b: 326. Cockerell, 1909c: 22. Zeuner and Manning, 1976: 208.

DIAGNOSIS: *Electrapis martialis* is most similar to *E. krishnorum* but differs by the presence of dense, plumose bands on the apical margins of the metasomal terga, the more distad position of 2rs-m in the forewing, and the more elongate first abscissa of M in the hind wing.

DESCRIPTION: **Female.** Total body length 8.30 mm; forewing length 6.38 mm. Head wider than long (length 2.55, width 3.10). Upper interorbital distance 1.65 mm; lower interorbital distance 1.30 mm. Interocellar distance 0.50 mm; ocellocular distance 0.45 mm; median to lateral ocellus 0.20 mm. Intertegular distance 2.55 mm. Basal vein basad cu-a by two times vein width, straight; second abscissa Rs relatively straight; 1rs-m distad 1m-cu by six times vein width; 2rs-m confluent with 2m-cu; first submarginal cell shorter than combined lengths of second and third submarginal cells; posterior border of second submarginal cell 1.5 times length of anterior border; posterior border of third submarginal cell twice as long as anterior border, anterior border approximately equal to anterior border of second submarginal cell; pterostigma longer than wide, margin inside marginal cell straight; marginal cell bending away from wing apex by pterostigmal width, feebly appendiculate; hind wing with 13 distal hamuli arranged in a single, evenly spaced series.

Labrum smooth. Integument of face obscured by fine layer of Schimmel (setae visible extending out of this Schimmel and described below). Mesosoma finely imbricate and impunctate except ventrally on mesepisternum with small punctures separated by a puncture width and mesoscutum and scutellum with sparse, faint punctures separated by a puncture width or less. Metasomal terga and sterna finely imbricate and impunctate.

Color apparently dark brown without maculations. Wing membrane hyaline; veins brown.

Pubescence white. Labrum with scattered, erect, short, simple setae. Clypeus and supraclypeal area with scattered, moderate-length, simple setae, such setae more numerous on face and plumose, those setae of frons appearing to be dense enough to have obscured integument if it were not already obscured by fine layer of Schimmel. Setae on vertex quite long, fuscous, and with minute branches by comparison to those setae of frons. Mesoscutum with dense, long, erect, plumose setae partially obscuring integument. Tegula with short, appressed, simple setae, setae with a few minute branches. Scutellar setae very long (1.5–2 times length of those on mesoscutum, most setae as long as or longer than scutellum) and plumose; setae entirely obscuring view of metanotum and propo-

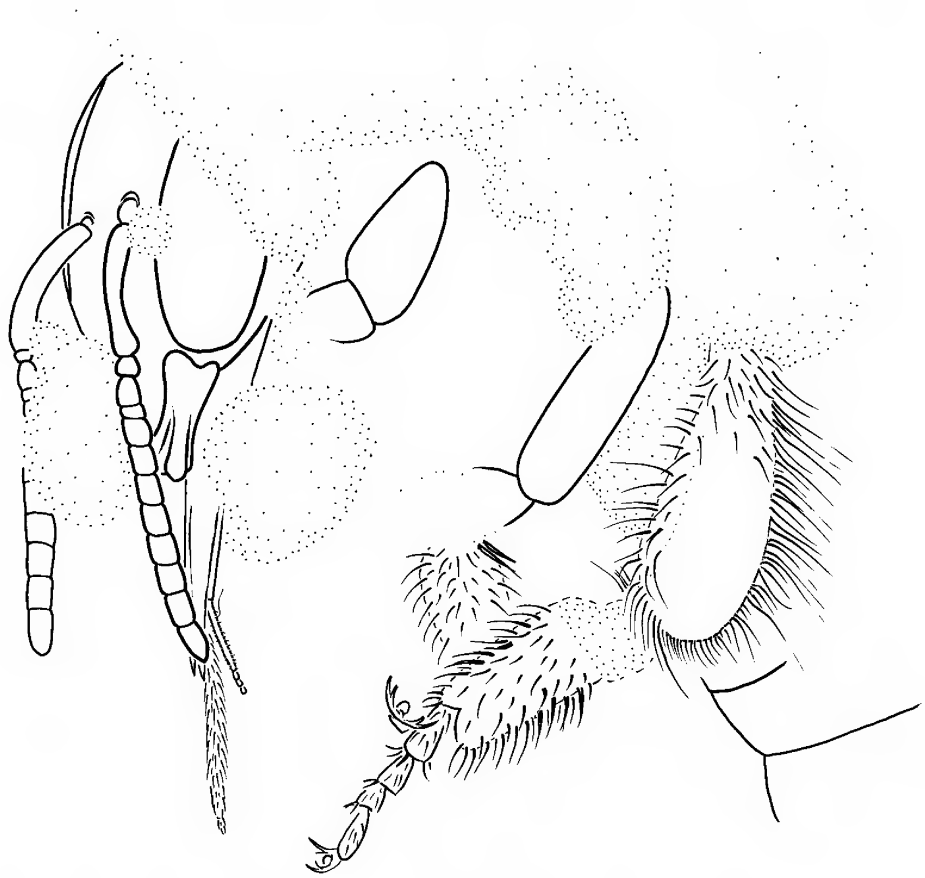


Fig. 65. Left lateral view of holotype female of *Electrapis krishnorum,* new species. Scale bar = 1 mm.

deum. Pleural pubescence long, dense, and plumose. Setae of legs long, numerous, and stiff on tibiae and tarsi, and mostly plumose; dense tuft of very long, sinuous, simple setae on ventral surface of mesotrochanter, setae of tuft directed posteriorly; corbicula with long, simple setae along lateral margins; sparse setae on outer metabasitarsus. Metasomal terga with sparse, minute, appressed, simple setae except on apical margins of T2–5 with bands of dense, short, plumose, suberect setae; sterna with scattered, short, erect or suberect, simple setae.

MATERIAL: Two total specimens. **Neotype (here designated).** Female, worker caste, B-JH 91 (AMNH) labeled "Neotype, *Chalcobombus martialis* Cockerell, desig. M. S. Engel" // "*Electrapis martialis* (Cockerell), det. M. S. Engel".

Non-type. Female, worker caste, Nr. 502 (CJDL) labeled: "Nr. 502" // "*Electrapis martialis* (Cockerell), det. M. S. Engel".

***Electrapis krishnorum*, new species**

Figures 65–67

Apis sp. Gerlach, 1989: 257. [misidentification]

DIAGNOSIS: This species is most similar to *E. martialis* in that both are relatively small by comparison to *E. meliponoides* and *E.*

tornquisti and both have pterostigmas that are longer than wide while lacking distinctive setal patches on their labra. From *E. martialis,* however, the new species differs by the absence of dense bands of plumose setae on the apical margins of T2–5, by the shortened first abscissa of M in the hind wing, and by the confluence of 2rs-m and 2m-cu in the forewing.

DESCRIPTION: **Female.** Total body length 9.30 mm; forewing length 6.40 mm. Head apparently wider than long (direct, frontal view of head not possible). Mandibular grooves weakened, those present appear to be (from upper to lower margin) acetabular groove, outer upper groove, and outer lower groove. Intertegular distance 2.15 mm. Basal vein basad cu-a by vein width, straight; second abscissa Rs relatively straight; 1rs-m distad 1m-cu by six times vein width; 2rs-m distad 2m-cu by vein width; first submarginal cell shorter than combined lengths of second and third submarginal cells; posterior border of second submarginal cell 1.25 times length of anterior border; posterior border of third submarginal cell nearly twice as long as anterior border, anterior border approximately equal to anterior border of second submarginal cell; pterostigma longer than wide, margin inside marginal cell slightly convex; marginal cell bending away from wing apex by slightly less than pterostigma width, feebly appendiculate; hind wing with 13 distal hamuli arranged in a single, evenly spaced series; first abscissa M slightly less than twice as long as rs-m.

Mandibular integument smooth except appearing minutely granular within weakened mandibular grooves. Labrum minutely granular. Clypeus and supraclypeal area with coarse, faint punctures separated by two times a puncture width or more, integument between smooth. Face, vertex, gena, and postgena smooth and impunctate. Mesosoma smooth and impunctate except ventrally on mesepisternum; posteriorly and laterally on mesoscutum and scutellum faint punctures separated by a puncture width or less. Metasomal terga and sterna finely imbricate and impunctate.

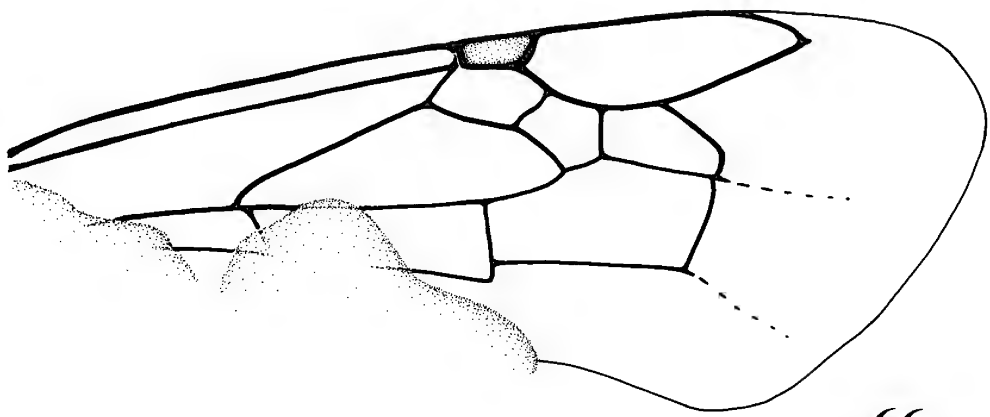
Color apparently dark brown, without maculations. Wing membrane hyaline; veins dark brown.

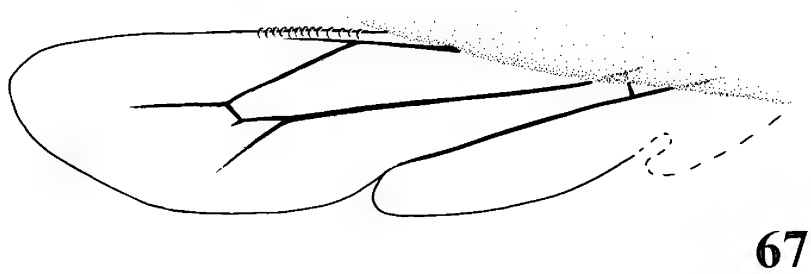
Pubescence silvery except those setae of vertex, tarsi, and apical terga slightly fuscous. Mandible with a few, very short, widely scattered, simple setae except lower margin with long, simple, scattered setae. Labrum with scattered, erect, short, simple setae. Clypeus and supraclypeal area with scattered, moderate-length, simple setae, such setae more numerous on face and some with a few, minute branches, those setae of face partially obscuring integument. Setae on vertex quite long, slightly fuscous, and with more minute branches than those setae of face. Scape with minute, simple, scattered, appressed setae. Postgena with scattered, long, erect, simple setae. Mesoscutum with dense, long, erect, plumose setae partially obscuring integument. Tegula with short, appressed, simple setae scattered on surface except anteriorly setae longer and with a few minute branches. Scutellar setae very long (at least 1.5 times length of those on mesoscutum, most setae as long as or longer than scutellum itself) and plumose; setae entirely obscure view of metanotum and propodeum. Pleural pubescence long, dense, and either simple or minutely plumose. Setae of legs long, numerous and stiff on tibiae and tarsi; dense tuft of very long, sinuous, simple setae on ventral surface of mesotrochanter, setae of tuft directed posteriorly; corbicula with long setae along lateral margins; stiff scattered setae on outer metabasitarsus and stiff comb rows on inner surface. Metasomal terga with sparse, minute, simple, appressed setae, terga without apical setal bands; sterna with scattered, short, erect, simple setae.

MATERIAL: Four specimens. **Holotype.** Female, worker caste, II1926 (BMNH) labeled: "II1926(1)" // "*Bombus*?, Baltic amber"// "*Electrapis*" // "Holotype, *Electrapis krishnorum* Engel".

Paratype. Female, worker caste, 5589 (ZMPA) labeled: "Muzeum Ziemi w Warszawie, 5589 (in two pieces), Apidae in Baltic Amber, Gerlach 1989: *Apis* L., *Electrapis*: det. Engel, Golarisk-Stogi, coll. T. Gierewicz, 1972" // "Baltic Amber, Eocene, 5589, Muzeum Ziemi Pan, M. S. Engel study" // "Paratype, *Electrapis krishnorum* Engel".

Paratype. Female, worker caste, Nr. 25 (CSUL) labeled: "Paratype, *Electrapis krishnorum* Engel".





Figs. 66–67. Wings of holotype female of *Electrapis krishnorum,* new species. **66.** Forewing. **67.** Hind wing. Scale bar = 1 mm.

Paratype. Female, worker caste, Nr. 71 (CJDL) labeled: "Nr. 71" // "Paratype, *Electrapis krishnorum* Engel".

ETYMOLOGY: The specific epithet is a patronymic honoring my dear friends and colleagues Drs. Kumar and Valerie Krishna, world's authorities on termites and medieval literature, respectively.

Electrapis tornquisti Cockerell

Electrapis tornquisti Cockerell, 1908b: 326. Cockerell, 1909c: 23. Zeuner and Manning, 1976: 231.

Electrapis hermenaui Bischoff *In* Kelner-Pillault, 1974: 624. *Nomen nudum* [= *Electrapis bombusoides* Kelner-Pillault, 1974].

Electrapis cockerelli Bischoff *In* Kelner-Pillault, 1974: 624. *Nomen nudum* [= *Electrapis bombusoides* Kelner-Pillault, 1974].

Electrapis cokerelli Kelner-Pillault, 1974: 624. *Lapsus calami.*

Electrapis bombusoides Kelner-Pillault, 1974: 625. NEW SYNONYMY.

DIAGNOSIS: *Electrapis tornquisti,* like *E. meliponoides,* is a larger species than *E. martialis* and *E. krishnorum.* The species can be distinguished from *E. meliponoides* by the longer pterostigma and the presence of medioapical patches of elongate setae on the labrum.

DESCRIPTION: **Female.** Total body length 15.16 mm; forewing length 9.17 mm. Head

longer than wide (length 4.41 mm, width 3.91 mm). Upper interorbital distance 2.72 mm; lower interorbital distance 2.09 mm. Basal vein basad cu-a by three times vein width, straight; second abscissa Rs relatively straight; 1rs-m distad 1m-cu by seven times vein width; 2rs-m distad 2m-cu by two times vein width; first submarginal cell shorter than combined lengths of second and third submarginal cells; posterior border of second submarginal cell 1.5 times length of anterior border; posterior border of third submarginal cell twice as long as anterior border, anterior border slightly less than length of anterior border of second submarginal cell; pterostigma longer than wide, margin inside marginal cell slightly concave; marginal cell bending away from wing apex by pterostigmal width, feebly appendiculate; hind wing with 17 distal hamuli arranged in a single, evenly spaced series; first abscissa M four times longer than rs-m.

Mandibular integument smooth except appearing minutely granular within weakened mandibular grooves. Labrum minutely granular. Clypeus and supraclypeal area with coarse, faint punctures separated by two times a puncture width or more, integument between smooth. Face, vertex, gena, and postgena finely imbricate and impunctate. Mesosoma finely imbricate and impunctate except some sparse, faint punctures on mesoscutum and scutellum. Metasomal terga and sterna finely imbricate; terga impunctate; S1–2 apparently impunctate, S3–5 minutely punctured on apical thirds, S6 minutely punctured on apical half, punctures on all sterna separated by 1–3 times a puncture width.

Color, where evident, dark brown without maculations. Wing membrane hyaline; veins black.

Pubescence white except those setae of protibia and tarsi black. Mandible with a few, very short, widely scattered, simple setae except lower margin with long, simple, scattered setae. Labrum with scattered, erect, short, simple setae and apical margin with mediolateral patches of elongate, simple setae. Clypeus and supraclypeal area with scattered, moderate-length, simple setae, setae more numerous on face and minutely plumose. Setae on vertex quite long, white (not fuscous as in *E. krishnorum*), and minutely plumose. Mesoscutum with dense, long, erect, plumose setae partially obscuring integument. Scutellar setae very long, dense, and plumose. Pleural pubescence long, dense, and minutely plumose. Setae of legs long, numerous, and stiff on tibiae and tarsi; inner surface of metafemur covered by keirotrichiae except medially this field narrows slightly; corbicula with long setae along lateral margins, inner surface of metatibia entirely covered by keirotrichiae; stiff scattered setae laterally on metabasitarsus, outer surface with sparse, simple setae, inner surface with comb rows. Metasomal terga with scattered, simple or minutely plumose setae, apical margins of terga with dense bands of short, plumose setae; sterna with scattered, erect, simple setae.

MATERIAL: Three specimens. **Neotype (*tornquisti*; here designated).** Female, worker caste, MB.I.1947 (ZMHB) labeled: "Neotype, *Electrapis tornquisti* Cockerell, desig. M. S. Engel [red label]". This is also the holotype specimen of *E. bombusoides* and bears additional labels reading: "*Electrapis bombusoides* n. sp., Holotype, S. Kelner-Pillault" // "Paläont. Mus. Berlin, coll. Kühl [actually from the Berendt collection]" // "*Electrapis hermanaui,* Bisch., Paratypus, 1930" // "*Elektrapis* [sic] *hermanaui,* 20" / / "Holotyp [sic], Paläontologisches Museum Berlin, *Electrapis bombusoides* Kelner-Pillault, 1974, slg. Berendt".

Holotype (*bombusoides*). Same specimen as neotype of *E. tornquisti* (above).

Paratype (*bombusoides*). Female, worker caste, MB.I.1948 (ZMHB) labeled: "27" // "Paratype, *Electrapis bombusoides*" // "MB.I.1948" // "Paratyp [sic], Paläontologisches Museum Berlin, *Electrapis bombusoides* Kelner-Pillault, 1974".

Non-type. Female, worker caste (IMGP) labeled: "*Electrapis bombusoides* n. sp., det. S. Kelner-Pillault [in Kelner-Pillault's handwriting]" // "*Electrapis cockerelli* Bisch., Paratype, 1930" // "*Electrapis cockerelli* Bisch., Paratypus, 1930" // "27 *Electrapis Cockerelli* [sic] Bisch., *Chalcobombus*? *humilis* Cockerell, *Electrapis bombusoides* S. Kelner P." // "60–21, *Electrapis bombuscoides* [sic] n. sp., Kelner-Pillault, Geologisch-Paläontologisches Institut Göttingen" //

"*Chalcobombus humilis* Cock. [stricken through], *Electrapis Cockerelli* [sic] Bisch.". This specimen is very poorly preserved and is only tentatively placed in *E. tornquisti.*

COMMENTS: At first notice the specimen from Göttingen labeled as *C. humilis* and then as *E. cockerelli* might be considered as the missing type of *C. humilis* and simply misinterpreted by Bischoff and Kelner-Pillault as *Electrapis.* However, *Chalcobombus* was defined as having a quadrangular metabasitarsus (among other features) and this is not the case with the fossil (the metabasitarsus being twice as long as broad; typical of *Electrapis*). I therefore concur with Bischoff and Kelner-Pillault that this cannot be Cockerell's missing type (a neotype for *C. humilis* is designated below). Moreover, the labels reading *Chalcobombus* are all in Bischoff's handwriting; none are in Cockerell's distinctive script.

Bischoff had originally intended to produce a paper on this material and to summarize the then known bees in Baltic amber under the title "Apiden des Bernsteins" (to have appeared in the 1939 volume of *Bernstein Forschungen*); however, this paper was never published. Kelner-Pillault subsequently borrowed this material from Berlin and prepared a description of Bischoff's specimens. At that time she mentioned the unpublished species names with which Bischoff had labeled the specimens (i.e., *E. hermenaui, E. cockerelli*). Under *Recommendation 50C* (ICZN, 1999b) authorship of these unavailable names should be attributed to Bischoff in Kelner-Pillault.

In Kelner-Pillault's (1974) illustration of the hind wing of the holotype female of *E. bombusoides* she omitted the jugal lobe and the wing drawing therefore strongly resembles that of a true bombine. The holotype specimen clearly has a jugal lobe present at the base of the hind wing; this structure is even more apparent in the specimen she chose as a paratype.

Electrapis meliponoides (Buttel-Reepen)

Figure 68

Plate 6c

Apis meliponoides Buttel-Reepen, 1906: 158.
Electrapis meliponoides (Buttel-Reepen); Cockerell, 1908b: 326. Cockerell, 1909b: 9. Zeuner and Manning, 1976: 229.

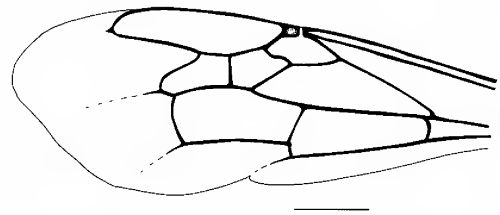


Fig. 68. Forewing of neotype female of *Electrapis meliponoides* (Buttel-Reepen). Scale bar = 1 mm.

DIAGNOSIS: *Electrapis meliponoides* is distinctive among all known *Electrapis* species for the shortened pterostigma. The species is large like *E. tornquisti* but lacks the medioapical patches of setae on the labrum.

DESCRIPTION: **Female.** Total body length 12.60 mm; forewing length 8.88 mm. Head longer than wide (length 2.85 mm, upper width 2.40 mm: lower width not preserved owing to damage to lower right of head). Intertegular distance 3.40 mm. Basal vein basad cu-a by vein width, straight; second abscissa Rs arched; 1rs-m distad 1m-cu by five times vein width; 2rs-m distad 2m-cu by four times vein width; first submarginal cell shorter than combined lengths of second and third submarginal cells; posterior border of second submarginal cell 1.25 times length of anterior border; posterior border of third submarginal cell twice as long as anterior border, length of anterior border slightly less than anterior border of second submarginal cell; pterostigma short, as long as wide, margin inside marginal cell slightly concave; marginal cell bending away from wing apex by nearly twice pterostigma width, feebly appendiculate; hind wing with 13 distal hamuli arranged in a single, evenly spaced series; first abscissa M 4.5 times as long as rs-m.

Preserved portion of facial integument obscured by fine layer of Schimmel; where evident, appearing imbricate. Mesosoma and metasoma, where evident, finely imbricate.

Color dark brown without maculations. Wing membrane hyaline; veins dark brown.

Pubescence white. Mandible with a few, very short, widely scattered, simple setae except lower margin with long, simple, scat-

tered setae. Labrum with scattered, erect, long, simple setae. Clypeus and supraclypeal area with scattered, moderate-length, simple setae, such setae more numerous on face and some with a few minute branches; those setae of face fairly dense and plumose. Setae on vertex quite long and simple. Genal setae as described for vertex except much shorter. Mesoscutum with dense, long, erect, plumose setae partially obscuring integument. Tegula with dense, long, appressed, plumose setae directed laterally. Scutellar setae as described for mesoscutum except along posterior third exceedingly long (longer than scutellum) and plumose. Pleural pubescence long, dense, and plumose. Setae of legs long, numerous and stiff on tibiae and tarsi; corbicula with long setae along lateral margins, setae of anterior margin simple, posterior margin minutely plumose; inner surface of metatibia entirely covered by keirotrichiae; stiff, elongate, scattered setae on lateral margins of metabasitarsus, outer surface with sparse, shorter, simple setae, inner surface with dense field of setae not arranged into rows. Metasomal terga with scattered, short, plumose setae, apparently with dense, apical bands on T2–5; sterna with scattered, long, erect or suberect, minutely plumose setae.

MATERIAL: One specimen. **Neotype (here designated).** Female, worker caste, B-JH 97 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Neotype, *Apis meliponoides* Buttel-Reepen, desig. M. S. Engel" // "*Electrapis meliponoides* (Buttel-Reepen), det. M. S. Engel".

Electrapis cf. *krishnorum*

MATERIAL: One specimen. **Non-type.** Female, worker caste, Nr. 501 (CJDL) labeled: "Nr. 501" // "*Electrapis* sp., det. M. S. Engel".

COMMENTS: This specimen represents a species near to *E. krishnorum* but has distinctive differences in both the wing venation as well as the mouthparts.

Electrapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female, worker caste, Nr. 577/2 (CHFG) labeled: "Nr. 577/2, Bittf. [Bitterfeld] Bernstein" // "*Electrapis* sp. indet., det. M. S. Engel".

Electrapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female?, Nr. 461 (GPUH) labeled: "Nr. 461 (Scheele), *Apis meliponoides* Buttel-Reepen = *Electrapis meliponoides* (Buttel-Reepen)" // "*Electrapis* sp. indet., det. M. S. Engel".

COMMENTS: This specimen was identified by Zeuner and Manning (1976) as belonging to *E. meliponoides* but the individual is entirely covered by fractures, Schimmel, and pyrite and such an indentification cannot actually be made. The size of the specimen is about that of *E. meliponoides.*

Electrapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female, worker caste, Nr. 19–00937 (CGHG) labeled: "Nr. 19–00937" // "*Electrapis* sp. indet., det. M. S. Engel".

Electrapis sp. indet.

MATERIAL: Three specimens. **Non-type.** Females worker caste? (CMGG) labeled: "*Electrapis* sp. indet., det. M. S. Engel".

Electrapis sp. indet.

MATERIAL: One specimen. **Non-type.** Female, worker caste, 3001 (GPUH) labeled: "*Electrapis* sp. indet., det. M. S. Engel, 1999".

COMMENTS: This individual is preserved with its dorsum at the amber surface and its mesosoma and metasoma opened. The internal sclerites are preserved and can be examined with some ease. The generic identification of the specimen is still possible owing to the relatively good preservation of the ventral half of the bee and it can be assigned to *Electrapis* with confidence. Specific identification, however, is not possible. It is from this individual that the above definition of the prosternal shape in *Electrapis* was made.

Genus *Protobombus* Cockerell

Protobombus Cockerell, 1908b: 326. Type species: *Protobombus indecisus* Cockerell, 1908b, monobasic [also designated by Cockerell,

1909b]. Cockerell, 1909b: 9. Manning, 1960: 306. Zeuner and Manning, 1976: 231.

Chalcobombus Cockerell, 1908b: 326. Type species: *Chalcobombus humilis* Cockerell, 1908b [= *Protobombus indecisus* Cockerell, 1908b], by designation of Cockerell, 1909b; isotypic with *Protobombus* Cockerell, 1908b by synonymy. Cockerell, 1909b: 11. Zeuner and Manning, 1976: 206. NEW SYNONYMY.

Sophrobombus Cockerell, 1908b: 326. Type species: *Sophrobombus fatalis* Cockerell, 1908b, monobasic [also designated by Cockerell, 1909c]. Cockerell, 1909c: 21. Zeuner and Manning, 1976: 213. NEW SYNONYMY.

DIAGNOSIS: Electrapine bees with a short, quadrangular metabasitarsus; similar in this respect to *Thaumastobombus* (described below). *Protobombus* differs from *Thaumastobombus* most notably, however, in the obtuse angle formed by the epistomal sulcus. Some *Protobombus,* like *Thaumastobombus,* have a superficial *Apis*-like habitus.

DESCRIPTION: Mandible with a few, weak apical teeth. Malar space shorter than basal mandibular width. Epistomal sulcus forming obtuse angle (fig. 69). Inner margins of compound eyes parallel, not emarginate (fig. 69). F1 longer than F2, not longer than combined lengths of F2 and F3; F3 longer than F2. Preoccipital ridge rounded. Mesoscutal anterior border broadly rounded; scutellum projecting over metanotum and basal area of propodeum. Basal area of propodeum strongly declivitous. Keirotrichiate field not elevated; metatibial spur serrate or minutely ciliate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae; metabasitarsus as long as wide. Margin of pterostigma within marginal cell convex; marginal cell apex offset from wing margin by pterostigma width or slightly less, apex rounded and feebly appendiculate. Sting variable, usually not barbed (some specimens appear to have microscopic barbs).

COMMENTS: The genus *Sophrobombus* was regarded as a genus of Meliponini by Zeuner and Manning (1976) because the forewing venation was apparently "reduced". The type species, *Sophrobombus fatalis* Cockerell, is notable for the presence of only two submarginal cells owing to the apparent absence of 1m-cu (i.e., the second transverso-cubital vein in Cockerell's system) (Cockerell, 1908b, 1909c). The type specimen of *S. fatalis* has been lost but Zeuner and Manning (op. cit.) located a specimen in the Scheele Collection (presently in the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg) that matches Cockerell's description in all respects. This specimen is here designated as the neotype for *S. fatalis.* The presence of only two submarginal cells is not the same "forewing venation reduction" as is diagnostic for Meliponini. In meliponines the distal wing veins (i.e., 2rs-m and 2m-cu) are lost, the marginal cell is typically open, and frequently other veins are also missing or greatly reduced. None of these are true for *S. fatalis.* The presence of a single inner metatibial spur, of an auricle, a supra-alar carina, an inner tooth on the claw, as well as numerous other characters separate this species from the Meliponini. *Sophrobombus* is actually an electrapine bee and similar in all respects to species of *Protobombus,* differing only in the number of

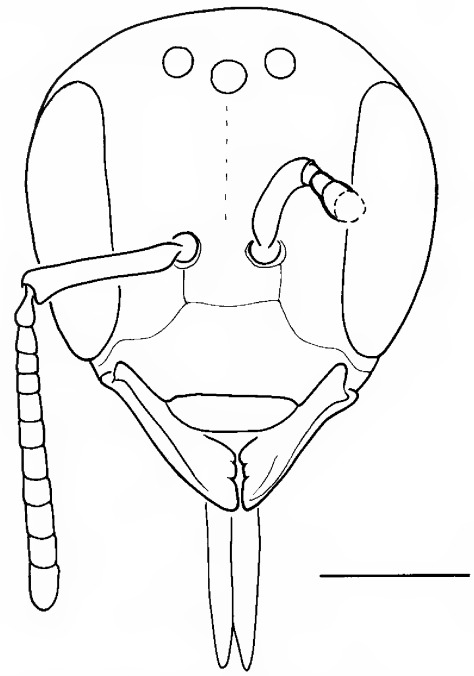


Fig. 69. Frontal view of head of neotype female of *Protobombus indecisus* Cockerell. Scale bar = 1 mm.

submarginal cells. Cockerell (1908b), who did not ally this species with the stingless bees (see fig. 120), separated *Sophrobombus* from *Protobombus* by the number of submarginal cells and by the basal vein being basad cu-a in the former. Below I describe a new species (*P. basilaris*) that blends the defining characters of the "genera" (i.e., basal vein basad cu-a but with three submarginal cells). I have therefore placed *Sophrobombus* as a junior synonym of *Protobombus.*

Chalcobombus was differentiated from *Protobombus* by the shape the pterostigma as well as the third submarginal cell. The shape of the third submarginal cell varies among the species of Electrapini and, although species-specific characters can be identified, these differences in shape are not correlated with other structural characters. Similarly, the shape of the pterostigma is quite variable and was incongruent with all other characters (including the shape of the third submarginal cell!). *Chalcobombus* appears to be synonymous with *Protobombus.*

Key to Species of *Protobombus*

1. Forewing with three submarginal cells (i.e., 1rs-m present) (figs. 75, 77) 2
– Forewing with two submarginal cells (i.e., 1rs-m absent) (fig. 74) .... *P. fatalis* (Cockerell)
2. Basal vein confluent with cu-a (fig. 77); hind wing with first abcissa of M approximately equal in length to second abcissa of M+Cu (fig. 73) 3
– Basal vein basad cu-a by twice vein width (fig. 75); hind wing with first abcissa of M distinctly shorter than second abcissa of M+Cu (fig. 76) ..... *P. basilaris,* n. sp.
3. Apical third of clypeus extending below lower tangent of compound eyes; keirotrichiate field of metatibial inner surface separated from metatibial apex by glabrous zone of variable length 4
– Clypeus not extending below lower tangent of compound eyes; keirotrichiate field of metatibial inner surface separated from metatibial apex by glabrous zone that is half width of keirotrichiate field in length .... *P. tristellus* Cockerell
4. Keirotrichiate field of metatibial inner surface separated from metatibial apex by glabrous zone that is half width of keirotrichiate field in length; posterior margin of third submaringal cell twice length of anterior border (fig. 77) ..... *P. hirsutus* (Cockerell)
– Keirotrichiate field of metatibial inner surface separated from metatibial apex by glabrous zone that is equal to width of keirotrichiate field in length (fig. 71); posterior margin of third submarginal cell thrice length of anterior border ..... *P. indecisus* Cockerell

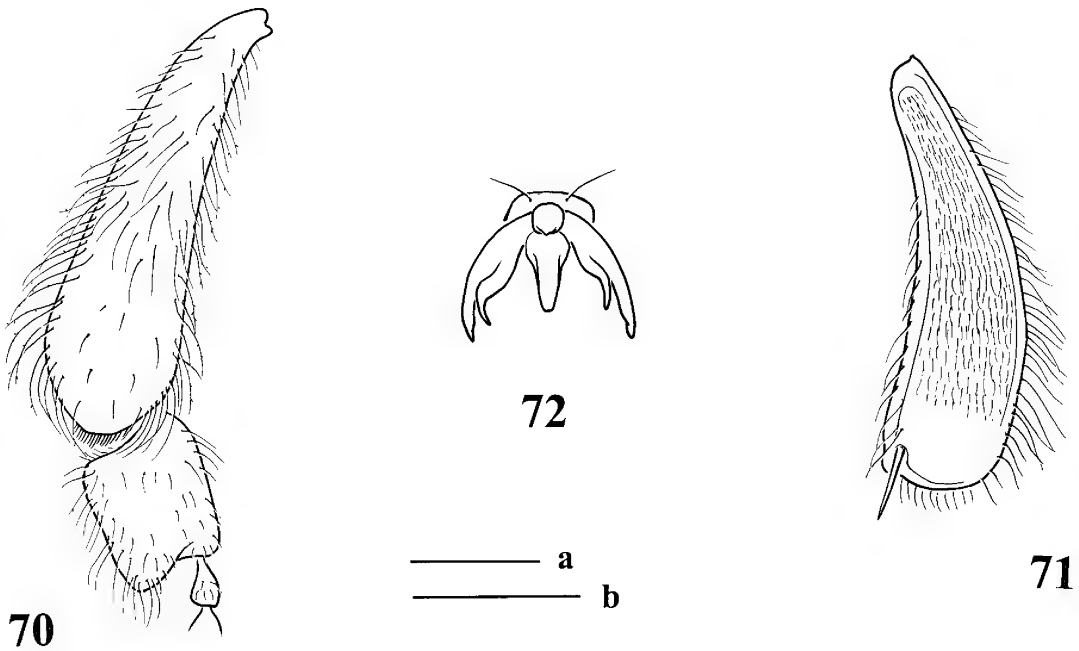
Protobombus indecisus Cockerell

Figures 69–73
Plate 6a,b

Protobombus indecisus Cockerell, 1908b: 326. Cockerell, 1909b: 10.
Chalcobombus humilis Cockerell, 1908b: 326. NEW SYNONYMY.
Electrapis (*Electrapis*) *apoides* Manning, 1960: 307. Zeuner and Manning, 1976: 227. NEW SYNONYMY.
Electrapis (*Protobombus*) *indecisus* (Cockerell); Zeuner and Manning, 1976: 232.

DIAGNOSIS: This species can be recognized by the combination of three submarginal cells, apical third of clypeus below lower tangent of compund eyes, and the keirotrichiate field on the inner surface of the metatibia separated from metatibial apex by distance equal to its own apical width.

DESCRIPTION: **Female.** Total body length 8.31 mm; forewing length 7.38 mm. Head wider than long (length 2.34 mm, width 2.63 mm). Upper interorbital distance 1.56 mm; lower interorbital distance 1.50 mm. Interocellar distance 0.38 mm; ocellocular distance 0.38 mm; median to lateral ocellus 0.09 mm. Lower half of clypeus below lower tangent of compound eyes. Intertegular distance 2.15 mm (measured from second specimen in amber piece). Basal vein confluent with cu-a, straight; second abscissa Rs relatively straight; 1m-cu basad 1rs-m by seven times vein width; 2rs-m distad 2m-cu by three times vein width, strongly arched; anterior border of second submarginal cell approximately one-third length of posterior border; posterior border of third submarginal cell slightly more than twice length of anterior border, anterior border twice as long as anterior border of second submarginal cell; hind wing with 10 distal hamuli arranged in a single, evenly spaced series; hind wing with first abscissa M approximately equal in length to second abscissa M+Cu.



Figs. 70–72. Leg structures of neotype female of *Protobombus indecisus* Cockerell. **70.** Outer surface of metatibia and metabasitarsus. **71.** Inner surface of metatibia. **72.** Claw and arolium. Scale bars = 0.25 mm (a), 1 mm (b); (a = fig. 72; b = figs. 70, 71).

Labrum imbricate and impunctate. Clypeus with sparse, small, faint punctures, integument between faintly imbricate. Supraclypeal area, face, vertex, gena, and postgena with sparse, small, faint punctures, integument between smooth. Pronotum finely imbricate. Mesoscutum and scutellum with sparse, faint punctures, integument between faintly imbricate. Metanotum imbricate and impunctate. Pleura with sparse, small punctures, integument between finely imbricate. Propodeum faintly imbricate and impunctate. Corbicula smooth and impunctate. Metasomal terga and sterna finely imbricate.

Where evident integument dark brown and shining. Wing membrane very lightly fuscous; veins dark brown.

Pubescence golden. Labrum with short, scattered, erect, simple setae. Clypeus with scattered, short, simple, suberect setae inter-

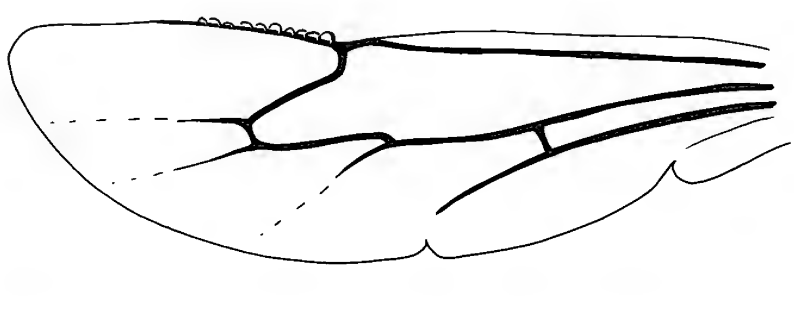


Fig. 73. Hind wing of neotype female of *Protobombus indecisus* Cockerell. Scale bar = 1 mm.

mixed with scattered, minute, appressed, simple setae. Face below level of antennal sockets with appressed, short, minutely plumose setae, setae numerous but not obscuring integument; supraclypeal area, vertex, gena, and remainder of face with scattered, simple, suberect or erect setae a few on vertex and gena with minute branches. Postgena with scattered, short, erect, simple setae. Pronotum with sparse, short, suberect simple setae except along posterior border and covering pronotal lobe with moderately long, erect, dense, plumose setae. Mesoscutum with scattered, short to moderate length, erect, minutely plumose setae. Tegula with short, scattered, minutely plumose setae anteriorly, posteriorly with minute, simple setae. Scutellar setae as described for mesoscutum except setae dense on posterior border and on axilla. Metanotum with sparse, minute, appressed, simple setae. Pleura with short, scattered, erect, simple setae except a few with minute branches. Lateral and posterior surfaces of propodeum as described for pleura except setae minute; basal area of propodeum without pubescence. Corbicular setae mostly simple but a few minutely plumose also with a few minute setae on corbicular surface itself (fig. 70), inner surface of metatibia mostly covered by keirotrichiate field, field separated from metatibial apex by length approximately equal to its width; metabasitarsus with scattered, short, simple setae, posterior edge with longer setae, inner surface with 5–6 comb rows. Metasomal terga with sparse, minute, appressed, simple setae; sterna with suberect to erect, moderately long, scattered setae, each with a few minute branches, setae entirely postgradular.

MATERIAL: Four specimens. **Neotype (*indecisus*; here designated).** Female, worker caste, B-JH 98 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Neotype, *Protobombus indecisus* Cockerell, desig. M. S. Engel". There are two individuals in the same block of amber; the neotype is the one figured in plate 6b and the right-hand bee in plate 6a.

Neotype (*humilis*; here designated). Same specimen as the neotype of *P. indecisus* (above); bears one additional label reading: "Neotype, *Chalcobombus humilis* Cockerell, desig. M. S. Engel".

Holotype (*apoides*). Female, worker caste (MNHN). Not seen. I have based my identification on photographs of the holotype specimen as well as illustrations of the wing venation and descriptive notes given by both Manning (1960) and Kelner-Pillault (1970a). From this information it is quite clear that *E. apoides* does not belong in *Electrapis* (see comments below) and is, in fact, conspecific with the specimen designated above as the neotype for *P. indecisus.*

Non-type. Female, worker caste, B-JH 98 (AMNH) preserved in same piece with neotype (see above).

Non-type. Female, worker caste, Nr. 1521 (CCGG) labeled: "Nr. 1521" // "*Protobombus indecisus* Cockerell, det. M. S. Engel".

COMMENTS: Although I was not able to examine the holotype of *E. apoides,* the placement of this species in *Protobombus* is simple owing to the quadrate metabasitarsus not only described in the original paper by Manning (1960) and by Zeuner and Manning (1976), but also nicely depicted in the published photograph of the holotype by Kelner-Pillault (1970a). Additionally, the confluence of the basal vein among other characters clearly shown in the photograph all suggest that this species is conspecific with Cockerell's *P. indecisus.* The line illustrations of the wing venation presented by Kelner-Pillault (1970b) are quite poor and I have not trusted them, instead referring to the descriptions and other illustrations. In fact, the holotype of *E. apoides* agrees quite well with not only Cockerell's descriptive notes about *P. indecisus* but also with the specimens designated here as neotypes. I therefore feel confident in the above synonymy.

Protobombus fatalis (Cockerell), new combination

Figure 74

Sophrobombus fatalis Cockerell, 1908b: 326. Cockerell, 1909c: 21. Zeuner and Manning, 1976: 214.

DIAGNOSIS: This species is immediately recognizable for the complete absence of 1rs-m in the forewing thus forming only two submarginal cells (fig. 74). The basal vein is basad cu-a and therefore resembles to some

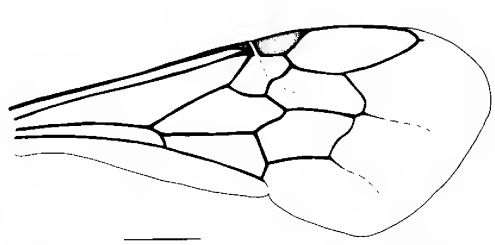


Fig. 74. Forewing of neotype female of *Protobombus fatalis* (Cockerell). Scale bar = 1 mm.

degree *P. basilaris*. The mandible of *P. fatalis* bears a strong, broad subapical tooth (see Material and Comments, below).

DESCRIPTION: **Female.** Total body length 5.82 mm; forewing length 3.91 mm. Head slightly wider than long (length 1.91 mm, width 1.94 mm). Mandible with strong, broad subapical tooth; tooth separated from remainder of the apical mandibular margin by deep incision. Interocellar distance 0.38 mm; ocellocular distance 0.34 mm; median to lateral ocellus 0.16 mm. Intertegular distance 1.59 mm. Basal vein basad cu-a by three times vein width, straight; second abscissa Rs arched; 1m-cu distad second abscissa Rs by seven times vein width; 2rs-m distad 2m-cu by three times vein width, strongly arched; second submarginal cell extremely elongate owing to absence of 1rs-m.

Face above antennal sockets, vertex and gena finely imbricate and impunctate. Pronotum finely imbricate and impunctate. Mesoscutum and scutellum faintly imbricate and impunctate. Mesepisternum sculptured as on mesoscutum. Corbicula smooth and impunctate. Metasomal terga and sterna finely imbricate.

Coloration not preserved. Wing membrane hyaline; veins brown.

Pubescence whitish. Face above level of antennal sockets and vertex with scattered, simple or minutely branched, erect setae. Gena with sparse, minute, appressed, simple setae. Pronotum with sparse, short, suberect, simple setae except along posterior border and covering pronotal lobe with moderately long, erect, dense, plumose setae. Mesoscutum with scattered, short to moderate length, erect, minutely plumose setae. Tegula with short, scattered, minutely plumose setae anteriorly, posteriorly with minute, simple setae. Scutellar setae as described for mesoscutum. Mesepisternum with short, scattered, erect, simple setae except a few with minute branches. Corbicular setae mostly simple and sinuous, also with three elongate, simple, sinuous setae on corbicular surface, corbicula occupying glabrous region on lower four-fifths of metatibia, inner surface of metatibia covered by keirotrichiate field, field separated from metatibial apex by length approximately equal to its width; metabasitarsus with scattered, short, simple setae, posterior edge with longer setae, inner surface with seven comb rows. Metasomal terga with sparse, minute, appressed, simple setae; sterna with suberect, moderately long, scattered, simple setae, setae entirely postgradular.

MATERIAL: Two specimens. **Neotype (here designated).** Female, Nr. 1225 (GPUH) labeled: "Neotype, *Sophrobombus fatalis* Cockerell, desig. M. S. Engel" // "Geol.-Paläont. Inst. Univ. Hamburg, Nr. 1225 (Scheele) *Sophrobombus fatalis* Cockerell" // "*Protobombus fatalis* (Cockerell), det. M. S. Engel, 1999". This specimen is poorly preserved with the ventral portion of the head lost into a series of fractures that eventually lead into a cavity on the lower surface of the amber piece. This cavity appears to open into what would have been the lowermost portion of the head and the anteroventral area of the mesosoma. In addition, numerous small fracture planes and fine layers of Schimmel obscure various structures of the bee. It can still, however, be placed confidently into the species as defined by Cockerell owing to the preservation of the metatibia, metabasitarsus, and forewing venation, all of which indicate this specimen to be conspecific with Cockerell's original material.

Non-type. Female, collection of Michael Bäätjer (Hamburg, Germany) labeled: "*Protobombus fatalis* (Cockerell), det. M. S. Engel, 2000". Although this specimen is in better condition than the neotype, it is part of a private collection and is presently available for purchase; thus, the final depository of this specimen remains unknown. In the interest of stability I have therefore chosen the less perfect individual to serve as the neotype since the whereabouts of this specimen will certainly change in the coming months and years rendering it difficult, if not impossible,

to locate again. This specimen was received at the time when the remainder of the manuscript was going to press. It was therefore not possible to prepare illustrations. In all comparable features this specimen is conspecific with the neotype designated above. The abdomen is unfortunately distended and portions of the legs and mesosoma cleared in preservation but is otherwise a nice specimen. It is from this specimen that information on the mandibular structure of *P. fatalis* was extracted. Similarly, information on the structure of other characters (e.g., the epistomal sulcus) can all be seen in this individual and confirms the placement of *P. fatalis* in the Electrapini and *Protobombus*. Furthermore, the information provided by this new material helps to reinforce the identity of the neotype as well as this specimen for being conspecific with Cockerell's (1908b, 1909c) missing original material.

COMMENTS: The specimen I studied was the same one examined by Zeuner and Manning (1976); see comments above for synonymy of the genus *Sophrobombus* with *Protobombus*. Cockerell (1909c) noted that his monotypic *Sophrobombus* was very much like *Protobombus* and *Chalcobombus* (above considered as synonyms) but differed most notably by the presence of only two submarginal cells. The specimen described by Cockerell (1908b, 1909c) agrees in every respect with the one selected here as the neotype, particularly in the unique trait of having only two submarginal cells. Cockerell's original specimen lacked mandibular dentition (differing in this respect from the non-type specimen examined here); it is possible that the mandibles were simply worn or set close the the face where the large subapical tooth would be completely obscured (for instance, in the available specimen the labrum and clypeus totally cover the subapical tooth of one mandible while the other, more fully opened, displays this character nicely).

Protobombus basilaris, new species

Figures 75, 76

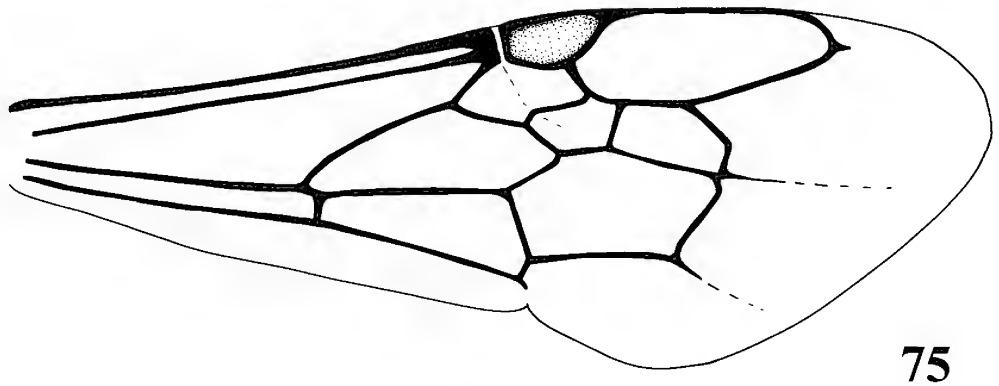
DIAGNOSIS: This species is notable for the position of the basal vein that is basad cu-a. *Protobombus fatalis* is similar in this respect but has only two submarginal cells.

DESCRIPTION: **Female.** Total body length 6.63 mm; forewing length 5.50 mm. Head wider than long (length 2.06 mm, width 2.38 mm). Interocellar distance 0.34 mm; ocellocular distance 0.34 mm; median to lateral ocellus 0.13 mm. Lower half of clypeus below lower tangent of compound eyes. Intertergular distance 1.72 mm. Basal vein basad cu-a by twice vein width, straight; second abscissa Rs arched; 1m-cu basad 1rs-m by seven times vein width; 2rs-m distad 2m-cu by vein width, strongly arched; posterior border of second submarginal cell approximately three times length of anterior border; posterior border of third submarginal cell 1.75 times length of anterior border, anterior border twice as long as anterior border of second submarginal cell; hind wing with 10 distal hamuli arranged in a single, evenly spaced series.

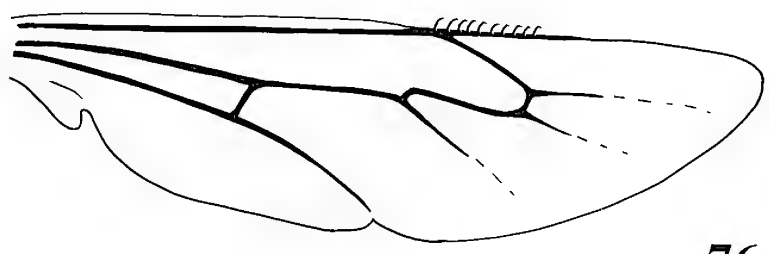
Labrum finely imbricate and impunctate; remainder of head and entirety of mesosoma and metasoma smooth and impunctate.

Integument dark brown and shining. Wing membrane hyaline; veins black.

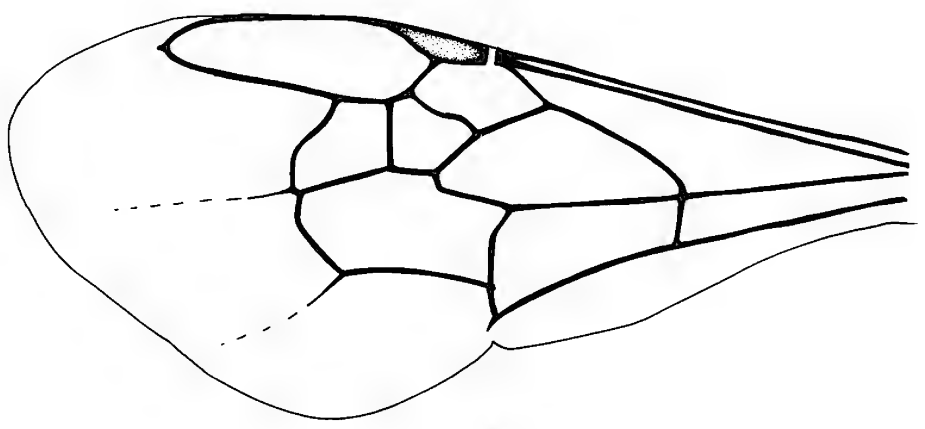
Pubescence whitish. Labrum with short, scattered, erect, simple setae. Clypeus with scattered, short, simple, suberect setae. Face, supraclypeal area, vertex, and gena with scattered, simple, suberect or erect setae, those on vertex and gena with minute branches. Pronotum with sparse, minute, suberect, simple setae except along posterior border and covering pronotal lobe with short, erect, plumose setae and a few elongate, plumose setae on dorsolateral angle that are slightly fuscous. Mesoscutum with scattered, short to moderate length, erect, minutely plumose setae. Tegula with sparse, appressed, minute setae. Scutellar setae as described for mesoscutum except setae dense and elongate on posterior border. Pleura with short, scattered, erect, simple setae. Lateral and posterior surfaces of propodeum as described for pleura except setae minute; basal area of propodeum without pubescence. Corbicular setae mostly simple but a few minutely plumose also with a few minute setae on corbicular surface itself, inner surface of metatibia mostly covered by keirotrichiate field, field separated from metatibial apex by length approximately equal to its width; metabasitarsus with scattered, short, simple setae, pos-



75



76



77

a

b

Figs. 75–77. Wings of *Protobombus* species. **75.** Forewing of *Protobombus basilaris,* new species. **76.** Hind wing of *P. basilaris,* new species. **77.** Forewing of *P. hirsutus* (Cockerell). Scale bars = 1 mm (a = fig. 76; b = figs. 75, 77).

terior edge with longer setae. Metasomal terga with sparse, minute, appressed, simple setae; sterna with suberect to erect, short, scattered setae, each with a few minute branches, setae entirely postgradular.

MATERIAL: One specimen. **Holotype.** Female, worker caste, MB.I.1939 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1939 (No. 36)" // "36 [handwritten label]" // "Holotype, *Protobombus basilaris* Engel".

ETYMOLOGY: The specific epithet is the Greek word *basilaris,* meaning "at the base", and is a reference to the basal position of the basal vein relative to cu-a.

Protobombus tristellus Cockerell

Protobombus tristellus Cockerell, 1909c: 24.
Electrapis (*Protobombus*) *tristellus* (Cockerell); Zeuner and Manning, 1976: 233.

DIAGNOSIS: This species is similar to *P. indecisus* and *P. hirsutus* but can be distinguished from both by the apical margin of the clypeus not extending below the lower tangent of compound eyes.

DESCRIPTION: **Female.** Total body length 6.13 mm; forewing length 5.13 mm. Head wider than long (length 1.78 mm, width 2.31 mm). Upper interorbital distance 1.47 mm; lower interorbital distance 1.25 mm. Interocellar distance 0.44 mm; ocellocular distance 0.39 mm; median to lateral ocellus 0.09 mm. Lower third of clypeus below lower tangent of compound eyes. Intertegular distance 1.72 mm. Basal vein confluent with cu-a, straight; second abscissa Rs arched; 1m-cu basad 1rs-m by six times vein width; 2rs-m confluent 2m-cu, strongly arched; posterior border of second submarginal cell 2.5 times length of anterior border; posterior border of third submarginal cell twice length of anterior border, anterior border 1.5 times as long as anterior border of second submarginal cell.

Labrum imbricate and impunctate. Clypeus with small, faint punctures separated by 1–2 times a puncture width, integument between smooth. Supraclypeal area, face, vertex, gena, and postgena with sparse, small, faint punctures, integument between smooth. Pronotum smooth and impunctate. Mesoscutum and scutellum with sparse, faint punctures, integument between smooth. Pleura with sparse, small punctures, integument between smooth. Propodeum smooth and impunctate. Corbicula smooth and impunctate. Metasomal terga smooth and impunctate; sterna finely imbricate and impunctate except apical margins more strongly imbricate.

Where evident, integument dark brown and shining. Wing membrane hyaline; veins dark brown.

Pubescence whitish. Labrum with short, scattered, erect setae. Clypeus with scattered, short, simple, suberect setae intermixed with scattered, minute, appressed, simple setae. Face below level of antennal sockets with appressed, short, minutely plumose setae, setae numerous but not obscuring integument; supraclypeal area, vertex, gena, and remainder of face with scattered, suberect or erect, simple setae, setae of vertex and gena with minute branches. Postgena with scattered, short, erect, simple setae. Pronotum with sparse, short, suberect, simple setae except those of dorsolateral angle and pronotal lobe dense, moderately long, erect, and plumose setae. Mesoscutum with scattered, short, erect, minutely plumose setae. Tegula with sparse, appressed, scattered, minutely plumose setae. Scutellar setae as described for mesoscutum except setae dense and elongate on posterior border. Mesepisternum with moderately long, scattered, erect, simple setae and intermixed with scattered, minute, appressed, simple setae; hypoepimeral area without longer setae, only with minute, appressed setae; metepisternum with setae as on mesepisternum except simple and distinctly more dense on dorsal half than on ventral half. Setae of lateral and posterior surfaces of propodeum as described for ventral half of metepisternum except setae minute; basal area of propodeum without pubescence. Corbicular setae minutely plumose, inner surface of metatibia mostly covered by keirotrichiate field, field separated from metatibial apex by length approximately equal to one-half its width; metabasitarsus with scattered, short, simple setae, posterior edge with longer setae, inner surface with seven comb rows. Metasomal terga with sparse, minute, appressed, simple setae, slightly longer on more apical terga; sterna with suberect to erect, short to moderately long, scattered setae, each with a few minute branches, setae entirely postgradular.

MATERIAL: One specimen. **Neotype (here designated).** Female, worker caste, MB.I.1943 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1943" // "50b [handwritten label]" // "Neotype, *Protobombus tristellus* Cockerell, desig. M. S. Engel".

Protobombus hirsutus (Cockerell), new combination

Figure 77

Plate 5d

Chalcobombus hirsutus Cockerell, 1908b: 326. Cockerell, 1909b: 12. Zeuner and Manning, 1976: 207.

DIAGNOSIS: This species is most similar to *P. indecisus* but differs by the separation of the keirotrichiate field from the metatibial apex being equal to one-half of its apical width and the posterior border of the third submarginal cell only twice as long as the anterior border.

DESCRIPTION: **Female.** Total body length 8.01 mm; forewing length 6.38 mm. Head wider than length (length 2.19 mm, width 2.25 mm). Upper interorbital distance 1.41 mm; lower interorbital distance 1.19 mm. Interocellar distance 0.44 mm; ocellocular distance 0.34 mm; median to lateral ocellus 0.13 mm. Lower half of clypeus below lower tangent of compound eyes. Intertegular distance 1.88 mm. Basal vein confluent with cu-a, straight; second abscissa Rs arched; 1m-cu basad 1rs-m by six times vein width; 2rs-m distad 2m-cu by vein width, strongly arched; posterior border of second submarginal cell approximately five times length of anterior border; posterior border of third submarginal cell 1.75 times length of anterior border, anterior border slightly more than twice as long as anterior border of second submarginal cell; hind wing with eight distal hamuli arranged in a single, evenly spaced series; hind wing with first abscissa M approximately equal in length to second abscissa M+Cu.

Labrum imbricate and impunctate. Clypeus with sparse, small, faint punctures, integument between faintly imbricate. Supraclypeal area, face, vertex, gena, and postgena with sparse, small, faint punctures, integument between smooth. Pronotum finely imbricate. Dorsum of mesosoma obscured by Schimmel and sundry small items of debris. Pleura impunctate finely imbricate. Corbicula with remains presumably of pollen covering surface. Metasomal terga and sterna finely imbricate.

Where evident, integument dark brown and shining. Wing membrane very lightly fuscous; veins dark brown.

Pubescence whitish or slightly fuscous. Labrum with short, scattered, erect, simple setae. Clypeus with scattered, short, simple, suberect setae intermixed with scattered, minute, appressed, simple setae. Face below level of antennal sockets with appressed, short, minutely plumose setae, setae numerous but not obscuring integument; supraclypeal area, vertex, gena, and remainder of face with scattered, simple, suberect or erect setae, a few on vertex and gena with minute branches. Postgena with scattered, short, erect, simple setae. Pronotum with sparse, short, suberect, simple setae except along posterior border and covering pronotal lobe with moderately long, erect, dense, plumose setae. Pubescence of mesosomal dorsal surface difficult to interpret, those mesoscutal setae appearing through layer of Schimmel and debris appearing to be scattered, moderate-length, erect, and minutely plumose; scutellar setae as described for mesoscutum except setae dense on posterior border and more elongate. Pleura with scattered, long, erect, simple setae. Lateral and posterior surfaces of propodeum as described for pleura except setae minute; basal area of propodeum without pubescence. Corbicular setae simple, inner surface of metatibia covered by keirotrichiate field, field separated from metatibial apex by length approximately equal to one-half its width; metabasitarsus with scattered, short, simple setae, posterior edge with longer setae. Metasomal terga with sparse, minute, appressed, simple setae; sterna with scattered, long, erect, fuscous, simple setae along apical margins.

MATERIAL: Four specimens. **Neotype (here designated).** Female, worker caste, B-JH 92 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Neotype, *Chalcobombus hirsutus* Cockerell, desig. M. S. Engel" // "*Protobombus hirsutus* (Cockerell), det. M. S. Engel".

Non-type. Female, worker caste (CJVG)

labeled: "*Protobombus hirsutus* (Cockerell), det. M. S. Engel".

Non-type. Female, worker caste, Nr. 1254 (CHFG) labeled: "Nr. 1254, Balt. Bernstein" // "*Protobombus hirsutus* (Cockerell), det. M. S. Engel".

Non-type. Female, worker caste, Nr. 1255 (CHFG) labeled: "Nr. 1255, Balt. Bernstein" // "*Protobombus hirsutus* (Cockerell), det. M. S. Engel".

Protobombus sp. indet.

MATERIAL: One specimen. **Non-type.** Female, Nr. 2608 (CCGG) labeled: "Nr. 2608" // "*Protobombus* sp. indet., det. M. S. Engel".

Protobombus sp. indet.

MATERIAL: One specimen. **Non-type.** Female, Nr. 1962.I.262 (BSPG): labeled "Bayer. St. Slg. Paläont. Hist. Geol. (BSP), Nr. 1962.I.262, Apidae, Honigbiene, Unteroligozän, Ostpreussen" // "*Protobombus* sp. indet., det. M. S. Engel, 1999".

COMMENTS: This specimen is in exceedingly poor shape. The bee is almost completely pyritized. The general habitus, presence of a corbicula, and quadrangular metabasitarsus suggests a species of *Protobombus.* The identity of this specimen will probably never be known with any reasonable degree of certainty.

***Thaumastobombus*, new genus**

TYPE SPECIES: *Thaumastobombus andreniformis* Engel, new species.

DIAGNOSIS: This group superficially resembles in its general habitus a short-tongued bee (either an andrenine, rophitine, or melittine) as well as the dwarf honey bees [Apini, *Apis* (*Micrapis*)] (fig. 78; pl. 5f). It, however, readily falls away from the former by being a long-tongued bee and a corbiculate apine at that. From the latter it differs in the tribal characters [Apini lacks metatibial spurs and outer mandibular grooves, has elongate eye hairs, an elongate malar space, among other features: refer to Engel (1999c) for a diagnosis of the honey bees and their constituent groups; however, note that in the subgeneric diagnoses for *Apis* presented in Engel (1999c), references to the shape of the first submarginal cell should refer to the *third* submarginal cell]. Among electrapines, *Thaumastobombus* is most similar to *Protobombus,* both sharing the quadrangular metabasitarsus. The former differs, however, by the linear epistomal sulcus and weakly emarginate compound eyes that converge below.

DESCRIPTION: Mandible with a few, weak apical teeth along upper half. Malar space short, shorter than basal mandibular width. Clypeus flat, not protuberant in lateral view. Epistomal sulcus linear (fig. 80). Inner margins of compound eyes slightly converging below, weakly emarginate (figs. 79, 80). F1 longer than F2, not longer than F2–3 combined; F3 longer than F2. Mesoscutal anterior border broadly rounded; median and parapsidal lines moderately impressed; scutellum projecting over metanotum and basal area of propodeum. Basal area of propodeum strongly declivitous (fig. 78). Keirotrichiate field not elevated; metatibial spur pectinate (figs. 83, 84); auricular basket dense, setae long (fig. 81); rastellum strong and formed of stiff setae (fig. 83); metabasitarsus about as long as wide (fig. 81). Margin of pterostigma within marginal cell convex; marginal cell apex offset from wing margin by slightly less than pterostigma width, apex appendiculate (fig 85). Worker gonostyli minutely setose at apices (fig. 78); sting not barbed (except see *Thaumastobombus* cf. *andreniformis*).

ETYMOLOGY: The new genus-group name is a combination of the Greek words *thaumastos* (meaning "wonderful") and *bombos* (meaning "buzzing"; a derivative of *bombylios* meaning "bumble bee"). The name is masculine.

***Thaumastobombus andreniformis*, new species**

Figures 78–85
Plate 5f

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 6.92 mm; forewing length 4.45 mm. Head slightly wider than long (length 1.62 mm, width 1.70 mm). Upper interorbital distance 1.10 mm; lower interorbital distance 0.80 mm. Interocellar distance 0.45 mm; ocello-

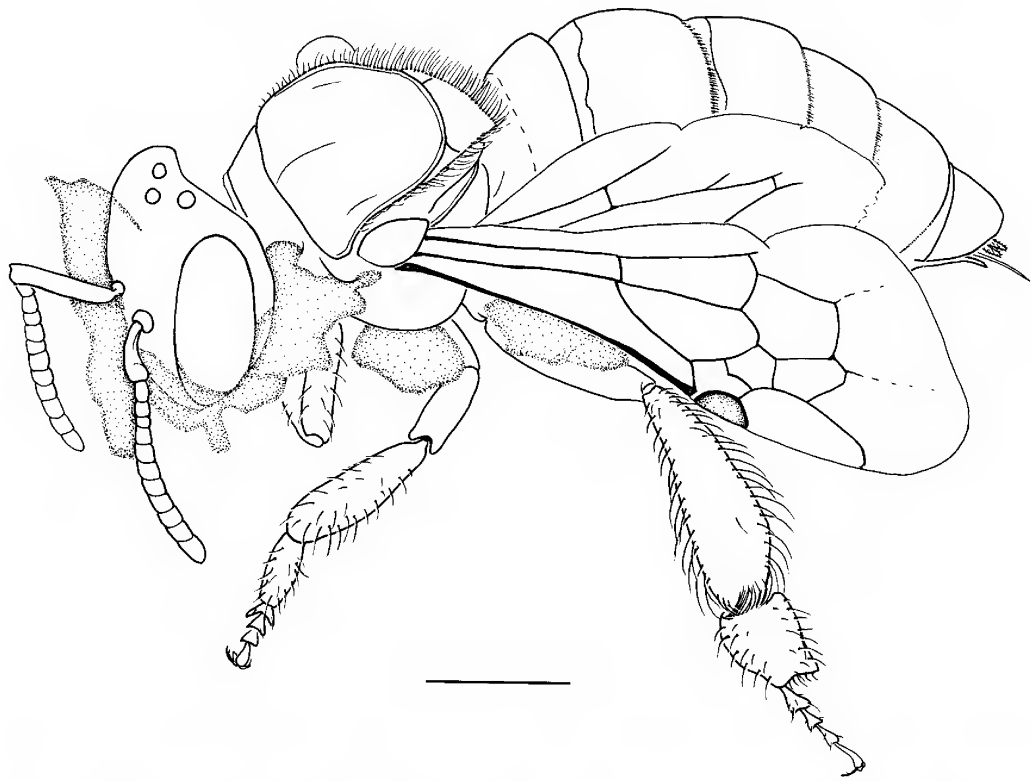


Fig. 78. Left dorsolateral habitus of holotype female of *Thaumastobombus andreniformis,* new species. Scale bar = 1 mm.

cular distance 0.25 mm; median to lateral ocellus 0.14 mm. Distal third of clypeus set below lower tangent of compound eyes. Intertegular distance 1.20 mm. Basal vein basad cu-a by vein width; 1rs-m distad 1m-cu by seven times vein width; 2rs-m distad 2m-cu by 2.5 times vein width; marginal cell apex separated from wing margin by one-half pterostigma width, feebly appendiculate; first submarginal cell shorter than second and third combined; second submarginal cell narrowed, anterior border just less than one-third length of posterior border, anterior border just less than one-half length of anterior border of third submarginal cell; anterior border of third submarginal cell just less than one-third length of posterior border; seven distal hamuli, arranged in a single, evenly spaced series.

Integument of head and mesosoma smooth and impunctate. Terga and sterna imbricate.

Coloration not well preserved, apparently black and shining except antennae, metasoma, and legs dark brown; without maculations. Wing membrane hyaline; veins strong and dark brown.

Pubescence generally pale. Labrum with sparse, simple, erect setae. Setae of face numerous, simple, appressed, and short, each with a few, minute branches, setae partially obscuring integument, such setae intermixed with sparse, erect, minutely branched setae; setae most dense on face below level of antennal sockets and lateral to clypeus; appressed setae disappearing by vertex and erect setae becoming gradually more numerous. Gena with appressed setae like those of face; postgena with sparse, erect, moderate-

Fig. 79. Frontal view of head of holotype female of *Thaumastobombus andreniformis,* new species.

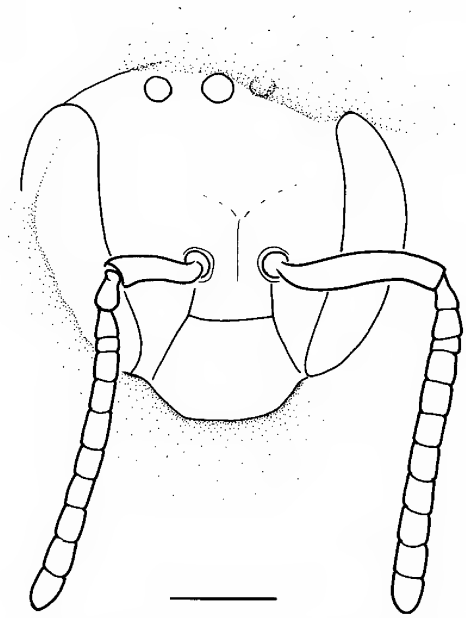


Fig. 80. Frontal view of head of holotype female of *Thaumastobombus andreniformis,* new species. Scale bar = 0.5 mm.

length, simple setae. Pubescence of mesoscutum as described for vertex. Tegula with a few, minute, appressed, simple setae. Scutellar pubescence as on mesoscutum except setae along posterior border elongate and plumose. Pleura with dense, long, plumose setae, partially obscuring integument. Posterior surface of metafemur with keirotrichiate zone on apical two-thirds; inner surface of metatibia with keirotrichiate zone not elevated but with narrow glabrous posterior margin that is one-fifth width of keirotrichiate zone, keirotrichiate zone separated from rastellum and metatibial apex by glabrous zone that is as long as width of keirotrichiate zone. Terga with sparse setal bands along apical margin, setae short and with a few, minute branches. Sterna with dense, apical bands of moderate to long, simple setae.

MATERIAL: One specimen. **Holotype.** Female, worker caste, B-JH 164 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Thaumastobombus andreniformis* Engel".

ETYMOLOGY: The specific epithet is a reference to the superficial habitus of the species that resembles a short-tongued bee. The species also resembles to some degree the dwarf honey bees (*A. florea* and *A. andreniformis*), which also resemble short-tongued bees.

Thaumastobombus cf. *andreniformis*

MATERIAL: Two specimens. **Non-type.** Two females, worker caste, Nr. 9 (CSUL) labeled: "*Thaumastobombus* cf. *andreniformis,* det. M. S. Engel".

COMMENTS: These two, well-preserved individuals differ slightly in the shape of the head and particularly in the structure of metatibial spur whereby the thickening of the spur toward its apex present in the holotype of *T. andreniformis* (fig. 84) is apparently absent in both of these individuals. This specimen also appears to have microscopic barbs on the sting (perhaps also present in true *T. andreniformis*?). These differences are likely not great enough to deserve specific status separated from *T. andreniformis*; however, I hesitate to place them immediately into *T. andreniformis* until more material of the genus is discovered. If these differences continue to be upheld or are found to be congruent with additional, yet undiscovered, characters, then specific status for this morph would be warranted.

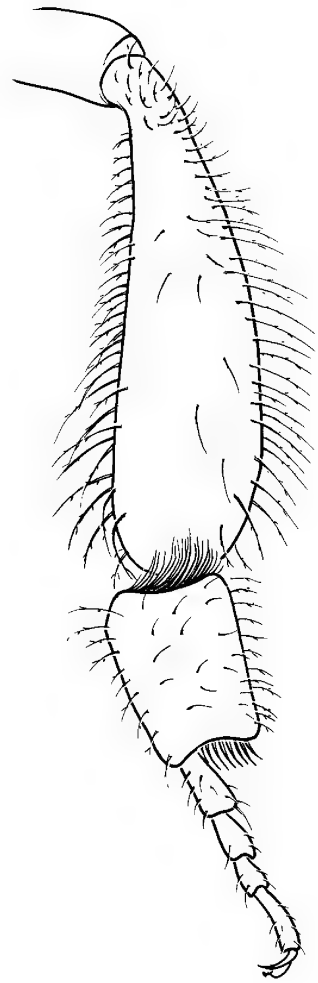
MELIKERTINI, New Tribe

TYPE GENUS: *Melikertes* Engel, 1998a.

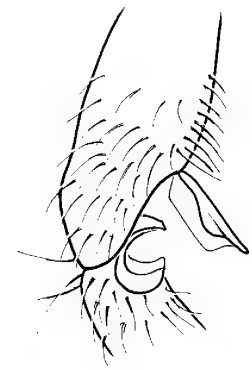
DIAGNOSIS: This group most closely resembles species of the stingless bee tribe Me-

→

Figs. 81–84. Leg structures of holotype female of *Thaumastobombus andreniformis,* new species. **81.** Outer surface of metatibia and metatarsus. **82.** Strigil at protibia-probasitarsus junction. **83.** Ventral, slightly oblique view of metatarsus and metatibia (thus, outer surface of metatibia is visible while inner surface of metabasitarsus is visible). **84.** Magnified view of metatibial spur. Scale bars = 0.5 mm (a = fig. 81; b = fig. 83; c = fig. 82).

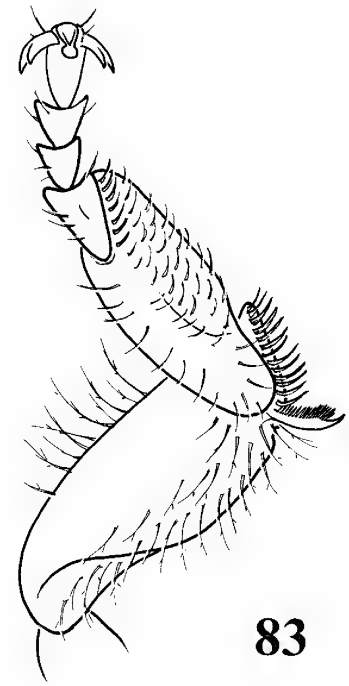


81



82

84



83

a

b

c

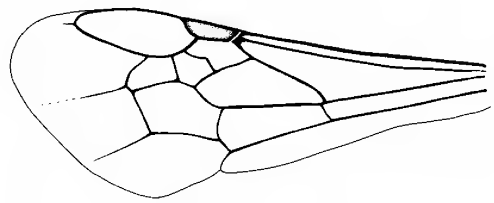


Fig. 85. Forewing of holotype female of *Thaumastobombus andreniformis,* new species. Scale bar = 1 mm.

liponini. The general habitus of all species is *Trigona*-like. The melikertines differ from the Meliponini by the complete wing venation, presence of a single metatibial spur, presence of a supraalar carina, toothed claws, presence of an auricle, and presence of a sting.

DESCRIPTION: Small to moderate size (ca. 3–8.5 mm long), slender, sparsely pubescent bees. Mandible without outer mandibular grooves. Labral width 3–4 times length. Clypeus gently convex and weakly protuberant in profile. Compound eyes bare. Supraälar carina present; scutellum broadly rounded posteriorly and variously produced (ranging from projecting over metanotum and propodeum to not projecting over metanotum). Claws of female with minute, inner tooth (figs. 89, 90, 108); arolium strong and present (e.g., fig. 108); single, reduced metatibial spur present (figs. 90, 102, 107); malus of strigilis with short anterior prong in addition to primary ventral velum; metabasitarsus with distinct auricle at base (figs. 89, 90, 106, 107); metatibia without penicillum. Distal venation of forewing strong and present (figs. 91, 103, 109); marginal cell large and narrowly rounded at apex, slightly offset from wing margin, feebly appendiculate, cell longer than distance from its apex to wing apex; pterostigma present and moderate size, much longer than prestigma, r-rs arising near or just beyond midpoint, margin within marginal cell convex; 1m-cu angled; hind wing with distinct jugal lobe, lobe broadly and deeply incised (figs. 92, 104, 110); hamuli reduced; wing membrane without alar papillae. Sting not reduced; apparently not barbed.

COMMENTS: This is a particularly diverse group of Baltic amber bees and specimens seem to be relatively commonly encountered. Table 9 summarizes the classification of the tribe as I have outlined it herein.

TABLE 9
Hierarchical Classification of Tribe †Melikertini

†TRIBE MELIKERTINI ENGEL
- Genus *Melissites* Engel
  - *Melissites trigona* Engel
- Genus *Melikertes* Engel
  - *Melikertes proavus* (Menge)
  - *Melikertes stilbonotus* (Engel)
  - *Melikertes clypeatus* Engel
- Genus *Roussyana* Manning
  - *Roussyana palmnickenensis* (Roussy)
- Genus *Succinapis* Engel
  - *Succinapis goeleti* Engel
  - *Succinapis micheneri* Engel
  - *Succinapis proboscidea* Engel

Key to Genera of Melikertini

1. Clypeal protrusion absent (e.g., figs. 100, 105) 2
– Clypeal protrusion present, i.e., base of clypeus produced into variously modified tubercles, tubercle bending upward over fronto-clypeal portion of epistomal sulcus and supraclypeal area, ending between antennal sockets (e.g., figs. 86–88, 93–98) . . . . . *Succinapis,* n. gen.
2. Scutellum bulging, overhanging metanotum and propodeum; apical margins of metasomal terga distinctly lighter than remainder of metasoma, thus metasoma appears banded; anterior and posterior margins of metabasitarus distinctly converging toward apex (fig. 107) 3
– Scutellum not bulging, not overhanging metanotum or propodeum (fig. 101); metasomal terga uniformly colored; anterior and posterior margins of metabasitarsus approximately parallel (fig. 102) . . . . . *Melikertes* Engel
3. Anterior margin of first submarginal cell inside marginal cell approximately equal to length of anterior margin of second submarginal cell inside marginal cell (i.e., vein r-rs as long as immediately succeeding abscissa of Rs) (fig. 109); basal vein confluent with cu-a; compound eyes converging below (fig. 105); F2 distinctly shorter than F3, F1 distinctly shorter than combined lengths

of F2–3 (fig. 105) . . . . . *Melissites,* n. gen.

– Anterior margin of first submarginal cell inside marginal cell many times longer than length of anterior margin of second submarginal cell inside marginal cell (i.e., vein r-rs many times longer than immediately succeeding abscissa of Rs); basal vein confluent with cu-a; compound eyes approximately parallel; F2 approximately equal in length to F3, F1 approximately equal to combined lengths of F2–3 . . . . . *Roussyana* Manning

Succinapis, new genus

TYPE SPECIES: *Succinapis proboscidea* Engel, new species.

DIAGNOSIS: This genus is most similar in general habitus to *Melikertes* but differs by the presence of a basal clypeal protrusion.

DESCRIPTION: Malar space short, shorter than basal mandibular width. Epistomal sulcus forming obtuse angle; clypeus with basal clypeal protrusion (i.e., base of clypeus slightly extending outward and upward over fronto-clypeal sulcus, typically covering supraclypeal area and ending in a tubercle between antennal sockets) (figs. 86–88, 93–98). F1 longer than F2; F2 equal to F3. Inner margins of compound eyes roughly parallel. Preoccipital ridge rounded. Mesoscutal anterior border broadly rounded; tegula tear-drop shaped; scutellum not bulging, not projecting over metanotum. Basal area of propodeum nearly horizontal, not declivitous. Keirotrichiate field not elevated (fig. 90); metatibial spur serrate or minutely ciliate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae (fig. 90); metabasitarsus parallel-sided. Three submarginal cells (fig. 91). Metasomal terga not banded.

ETYMOLOGY: The new genus-group name is a combination of the Latin words *succineus* (meaning "amber") and *apis* (meaning "bee"). The name is feminine.

COMMENTS: The peculiar clypeal protrusion is a unique feature among the corbiculate Apinae. At present the function of such a structure in workers is illusive.

Key to Species of *SUCCINAPIS*

1. Clypeal protrusion extending above level of antennal sockets by an antennal socket diameter or less (figs. 86–88, 93–95) 2

– Clypeal protrusion extending dorsally above level of antennal sockets by more than the diameter of an antennal socket (figs. 96–98) . . . . . *S. proboscidea,* n. sp.

2. Clypeal protrusion straight, apex not bent anteriorly, apex with short setae (figs. 86–88); mesepisternum smooth . . . . . *S. goeleti,* n. sp.

– Clypeal protrusion bent anteriorly at apex, apex with long setae (figs. 93–95); mesepisternum punctured . . . . . *S. micheneri,* n. sp.

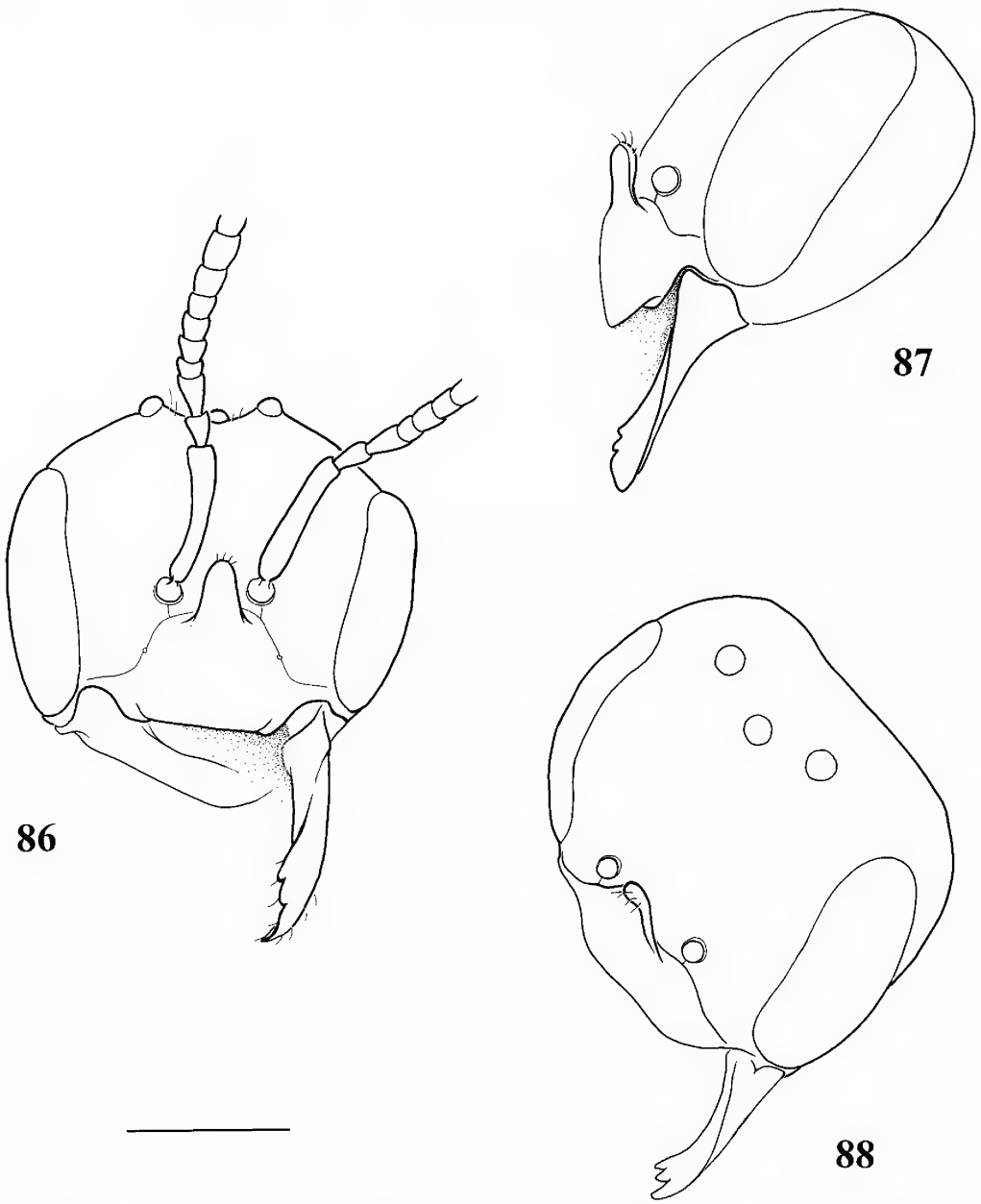
Succinapis goeleti, new species

Figures 86–92
Plate 7d

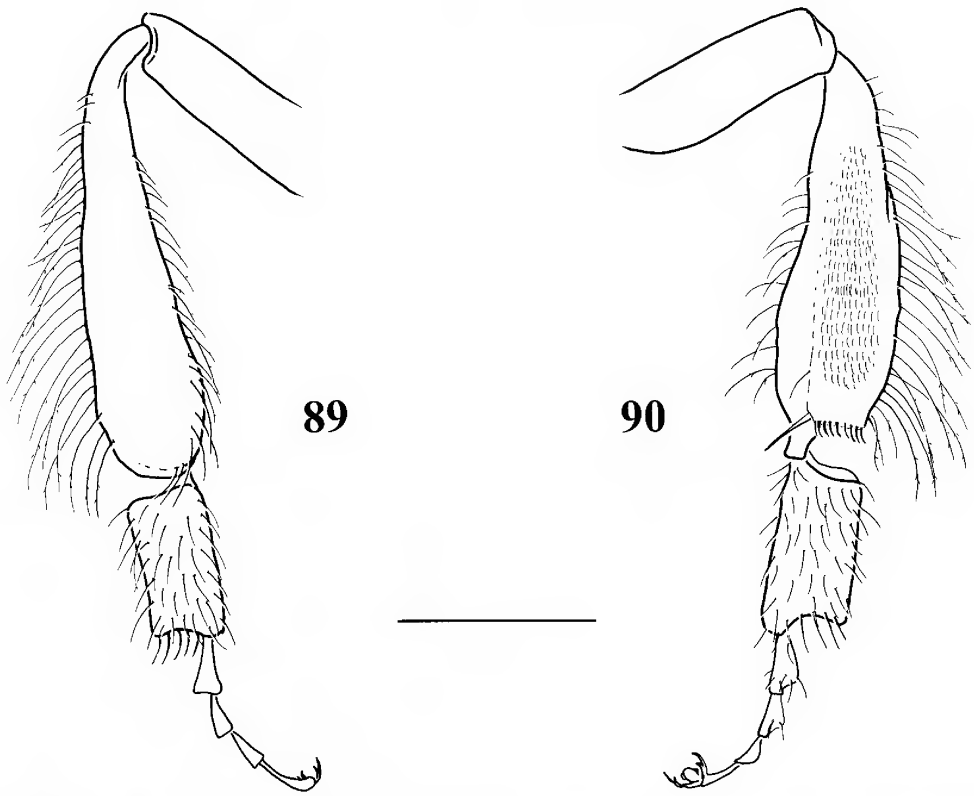
DIAGNOSIS: *Succinapis goeleti* is the most primitive species of the genus as it is presently understood (see phylogenetic discussion below; fig. 99). The species can be distinguished from all other *Succinapis* by the short clypeal protrusion that does not extend above the level of the antennae by more than the diameter of an antennal socket (figs. 86–88), the greatly narrowed second submarginal cell (fig. 91), and the impunctate pleura, among other features.

DESCRIPTION: **Female.** Total body length 3.55 mm; forewing length 3.30 mm. Head wider than long (length 0.93 mm, width 1.23 mm). Clypeal protrusion short, not extending dorsally above level of antennal sockets by more than diameter of an antennal socket (figs. 86–88), protrusion not bent anteriorly. Upper interorbital distance 0.92 mm; lower interorbital distance 0.82 mm. Interocellar distance 0.27 mm; ocellocular distance 0.32 mm; median to lateral ocellus 0.08 mm. Intertegular distance 0.78 mm. Basal vein basad cu-a by 2.5 times vein width; 1m-cu basad 2rs-m by five times vein width; 2rs-m distad 2m-cu by 1.5 times vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-tenth that of posterior border (i.e., second submarginal cell strongly narrowed anteriorly); length of posterior border of third submarginal cell 1.5 times that of anterior border, anterior border seven times length of anterior border of second submarginal cell; six distal hamuli, arranged in a single, evenly spaced series.

Clypeus impunctate and smooth. Face,



Figs. 86–88. Head of holotype female of *Succinapis goeleti,* new species. **86.** Frontal view. **87.** Lateral view. **88.** Frontodorsal, oblique view. Scale bar = 0.5 mm.

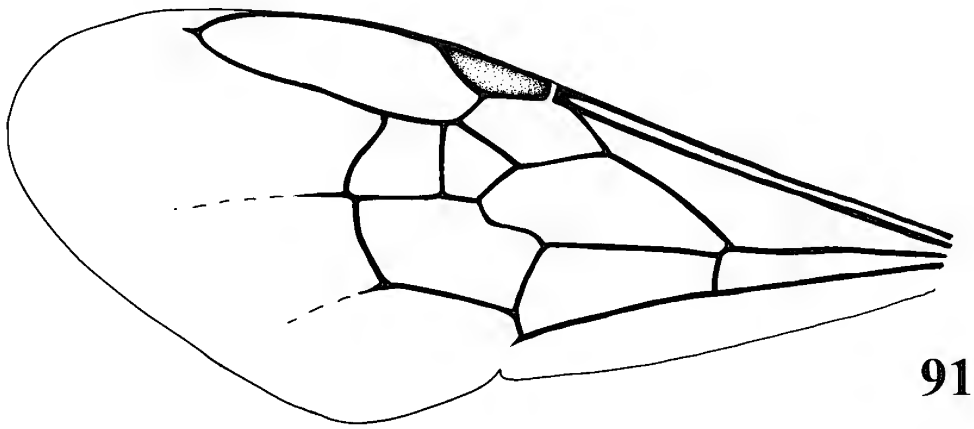


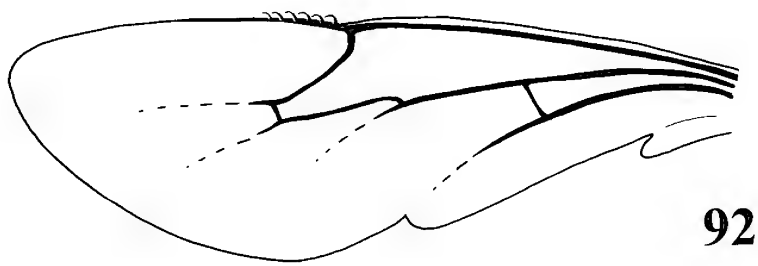
Figs. 89–90. Metatibia and metatarsus of holotype female of *Succinapis goeleti,* new species. **89.** Outer surface. **90.** Inner surface. Scale bar = 0.5 mm.

vertex, and gena with sparse, minute punctures, integument between smooth. Pronotum with sparse, faint, minute punctures, integument between smooth. Mesoscutum and scutellum sculptured as on mesoscutum. Tegula impunctate and smooth. Metanotum impunctate and faintly imbricate. Pleura impunctate and smooth. Propodeum glabrous. Metasoma impunctate and faintly imbricate.

Head, mesosoma, and metasoma black without maculations; legs dark brown. Wing membrane hyaline; veins strong and dark brown.

Pubescence fuscous. Labrum with moderate-length, simple, erect setae scattered on surface. Clypeus with sparse, minute, suberect, simple setae and short, simple, suberect, anteriorly-directed setae on dorsal-facing surface of clypeal protrusion. Face with sparse, suberect, minute, simple setae. Setae of vertex and gena as described for face. Postgena with short, simple, erect setae. Pubescence of pronotum as described for face. Mesoscutum with short, sparse, simple, erect setae. Scutellum with erect, long (2.5–4 OD) setae on posterior border, setae minutely plumose. Pleural pubescence as described for face. Lateral surface of propodeum with pubescence as described for face; basal area of propodeum without pubescence. Inner surface of metafemur and metatrochanter without pubescence except apical sixth of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate field, field separated by its width from metatibial apex; corbicula bordered by long, minutely-plumose setae; metatarsus with simple, stout setae; seven comb rows on inner surface of metabasitarsus. Metasomal terga with sparse, simple, short, appressed setae, slightly more





Figs. 91–92. Wings of holotype female of *Succinapis goeleti,* new species. **91.** Forewing. **92.** Hind wing. Scale bar = 0.5 mm.

numerous laterally; sterna with scattered, simple, erect (2.5–3 OD) setae.

MATERIAL: Two specimens. **Holotype.** Female, worker caste, B-JH 90 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Succinapis goeleti* Engel".

Paratype. Female, worker caste, B-W 162 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Paratype, *Succinapis goeleti* Engel".

ETYMOLOGY: The specific epithet is a patronymic honoring Mr. Robert G. Goelet, Chairman Emeritus of the AMNH Board of Trustees. Mr. Goelet has generously supported my work at the AMNH, while at the same time greatly augmenting the collection of living and amber-fossil insects. It is only fitting that one of these spectacular fossils bear his name.

Succinapis micheneri, new species

Figures 93–95

Plate 7c

Electrapis (*Roussyana*) *palmnickenensis* (Roussy); Zeuner and Manning, 1976: 233. [misidentification]

DIAGNOSIS: This species is similar to *S. goeleti* in that the clypeal protrusion is relatively short (not extending above the level of the antennae by more than the diameter of an antennal socket) but differs in that the apex of the process is bent anteriorly (fig. 93–95). Moreover, the second submarginal cell is not as strongly narrowed anteriorly

(the anterior border is only one-fourth that of the posterior border in *S. micheneri* by comparison to approximately one-tenth in *S. goeleti*) and the pleura are distinctly punctured.

DESCRIPTION: **Female.** Total body length 3.68 mm; forewing length 3.05 mm. Head wider than long (length 1.08 mm, width 1.13 mm). Clypeal protrusion short, not extending dorsally above level of antennal sockets by more than diameter of an antennal socket, protrusion strongly bent anteriorly (figs. 93–95). Upper interorbital distance 0.83 mm; lower interorbital distance 0.77 mm. Interocellar distance 0.25 mm; ocellocular distance 0.27 mm; median to lateral ocellus 0.07 mm. Intertegular distance 0.75 mm. Basal vein basad cu-a by 1.5 times vein width; 1m-cu bisecting second submarginal cell; 2rs-m distad 2m-cu by two times vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-fourth that of posterior border; length of posterior border of third submarginal cell 1.5 times that of anterior border, anterior border twice as long as that of second submarginal cell; six distal hamuli, arranged in a single, evenly spaced series.

Clypeus impunctate and smooth. Scape with sparse, minute punctures, integument between smooth. Face with minute punctures separated by 2–4 times a puncture width, integument between smooth. Sculpturing of vertex and gena as described for face. Postgena impunctate and smooth. Pronotum with minute punctures separated by a puncture width except medially punctures faint, integument between smooth. Mesoscutum with faint, sparse, minute punctures, integument between smooth. Scutellum sculptured as on mesoscutum. Tegula with minute, sparse, faint punctures, integument between smooth. Pleura with small punctures separated by 1–2 times a puncture width except hypoepimeral area impunctate, integument otherwise smooth between punctures. Sculpturing of propodeal lateral surface as described for mesepisternum; basal area of propodeum glabrous. Metasomal terga smooth and impunctate; sterna finely imbricate and impunctate.

Color, where evident, brown, without maculations. Wing membrane hyaline; veins strong and brown.

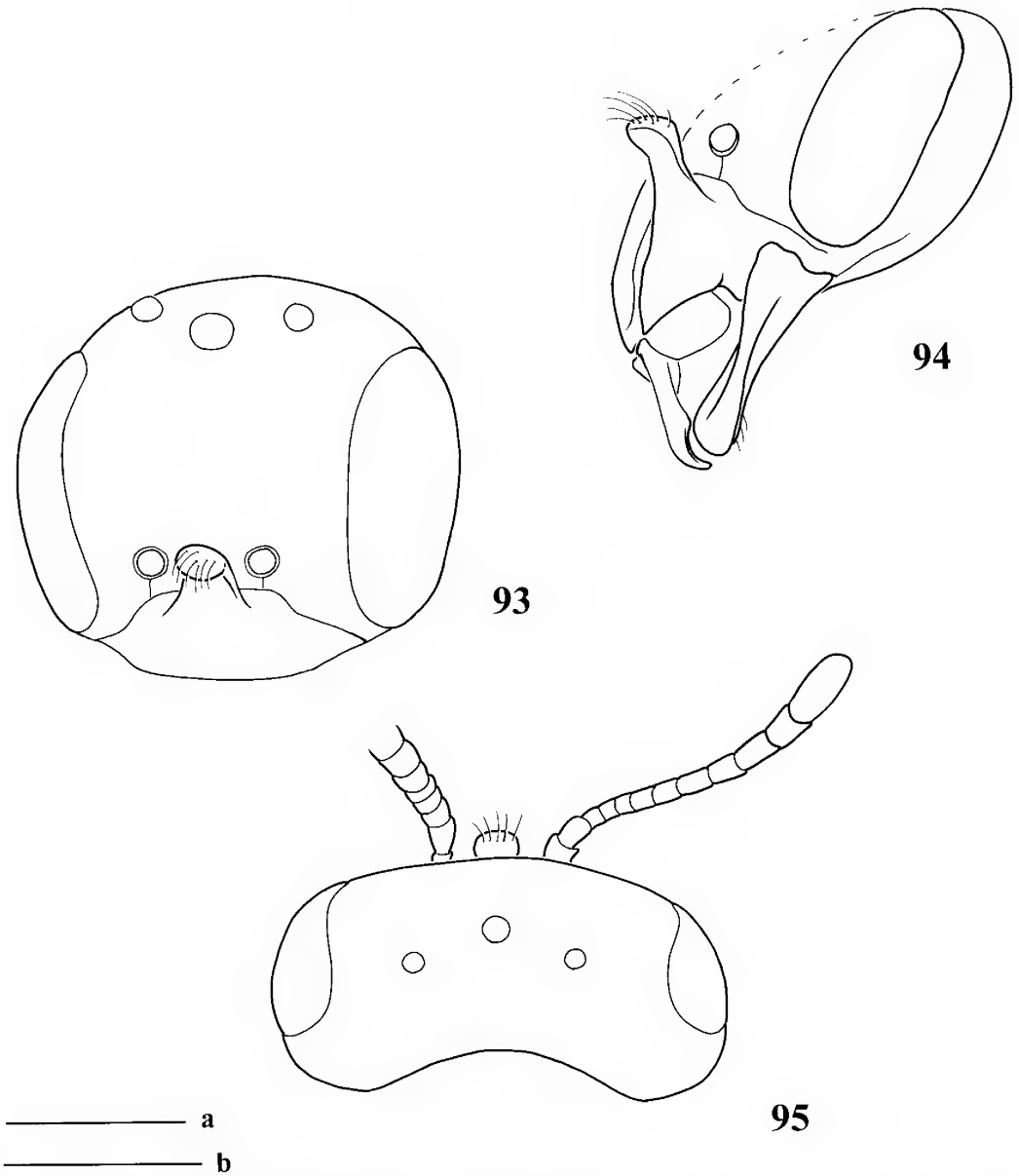
Pubescence generally whitish. Labrum with moderate-length, simple, erect setae scattered on integumental surface. Clypeus without setae except moderate-length, simple, suberect, anteriorly-directed setae on dorsal-facing surface of clypeal protrusion. Face with sparse, suberect, short, simple setae, setae more dense in lower paraocular area but not obscuring integument. Setae of vertex and gena as described for face except minute. Postgena with short, simple, erect setae. Pubescence of pronotum as described for face except setae of dorsal surface restricted to posterior border and minute. Mesoscutum with short, sparse, simple, erect setae. Scutellum with erect, long (1–3 OD) setae on posterior quarter, setae each with several minute branches and slightly fuscous. Hypoepimeral area without setae; remainder of pleura with pubescence as described for face. Lateral surface of propodeum with pubescence as described for face; basal area of propodeum without setae. Inner surface of metafemur and metatrochanter without pubescence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia mostly covered by field of keirotrichiae, field separated from metatibial apex by length equivalent to its own width; corbicula bordered by long, minutely-plumose setae; metatarsus with simple, stout setae; six comb rows on inner surface of metabasitarsus. Metasomal terga with scattered, simple, short, appressed setae, sparse on central discs; sterna with scattered, simple, suberect setae that are short on S1–2 (0.5–1 OD) then progressively longer on more apical sterna (reaching 2.5 OD by S5).

MATERIAL: Twenty-one specimens. **Holotype.** Female, worker caste, B-JH 103 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Succinapis micheneri* Engel".

Paratype. Female, worker caste, B-W 154 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Paratype, *Succinapis micheneri* Engel".

Paratypes. Five females, worker caste (CFEG) labeled: "Paratype, *Succinapis micheneri* Engel".

Paratype. Female, worker caste, Nr. 3709 (CCGG) labeled: "Paratype, *Succinapis micheneri* Engel".



Figs. 93–95. Head of holotype female of *Succinapis micheneri,* new species. **93.** Fronal view. **94.** Ventrolateral, oblique view. **95.** Dorsal view. Scale bars = 0.5 mm (a = fig. 93; b = figs. 94, 95).

Paratypes. Eleven females, worker caste (eight complete, three partials), Nr. 3–17 (CGHG) labeled: "Nr. 3–17" // "Paratype, *Succinapis micheneri* Engel".

Paratype. Female, worker caste, Nr. 80 (GPUH) labeled: "Nr. 80 (Scheele)" // "Erdbiene, Apidae, genus *Andrena*?" // "Paratype, *Succinapis micheneri* Engel". This is the specimen misidentified as *Electrapis* (*Roussyana*) *palmnickenensis* by Zeuner and

Manning (1976: see Comments under *Roussyana palmnickenensis,* below).

Paratype. Female, worker caste (PMUZ) labeled: "Paratype, *Succinapis micheneri* Engel".

ETYMOLOGY: The specific epithet is a patronymic honoring my mentor and friend, Dr. Charles D. Michener, world's authority on bees.

***Succinapis proboscidea*, new species**

Figures 96–98

Plate 7b

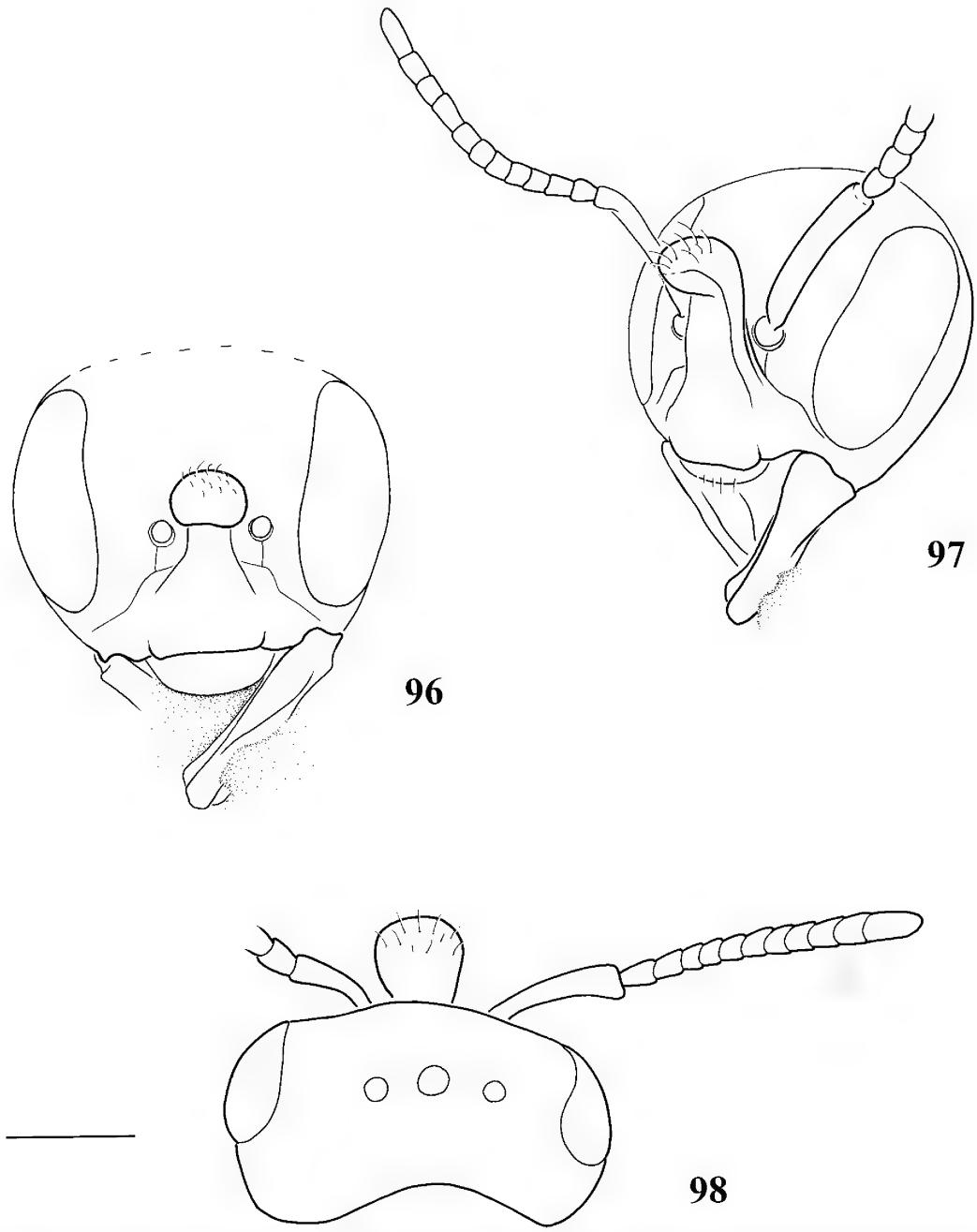
DIAGNOSIS: This is the most distinctive of all the *Succinapis* species. The grossly enlarged clypeal protrusion that is both bent anteriorly as well as extending above the level of the antennae by more than the diameter of an antennal socket (figs. 96–98) serves to immediately differentiate *S. proboscidea* from both *S. micheneri* and *S. goeleti.*

DESCRIPTION: **Female.** Total body length 4.15 mm; forewing length 3.55 mm. Head wider than long (length 1.34 mm, width 1.43 mm). Clypeal protrusion greatly enlarged, extending above level of antennal sockets by more than diameter of an antennal socket, protrusion bent anteriorly (figs. 96–98). Upper interorbital distance 0.98 mm; lower interorbital distance 0.93 mm. Interocellar distance 0.40 mm; ocellocular distance 0.30 mm; median to lateral ocellus 0.10 mm. Intertegular distance 0.98 mm. Basal vein basad cu-a by vein width; 1m-cu bisecting second submarginal cell; 2rs-m distad 2m-cu by two times vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-fourth that of posterior border; length of posterior border of third submarginal cell 1.75 times that of anterior border, anterior border two times length of that of second submarginal cell; six distal hamuli, arranged in a single, evenly spaced series.

Clypeus with sparse, minute punctures, integument between smooth; anterior-facing surface of clypeal protrusion with a few weak longitudinal striae. Scape with minute punctures separated by a puncture width, integument between smooth. Face with minute punctures separated by 1–2 times a puncture width, integument between smooth; punctures becoming gradually more faint and more sparse toward vertex and on gena. Pronotum with minute punctures separated by a puncture width except medially punctures faint, integument between smooth. Mesoscutum mostly obscured by a thin layer of Schimmel; where evident, integument with faint, minute punctures separated by 1–2 times a puncture width, integument between smooth. Scutellum sculptured as on mesoscutum. Tegula with minute, faint punctures on outer half, otherwise integument smooth. Metanotum obscured from view by fracture planes and flows from scutellum. Pleura with small punctures separated by 1–2 times a puncture width, becoming faint on central disc of mesepisternum and separated by 2–4 times a puncture width, and hypoepimeral area with faint and exceedingly sparse punctures, integument of pleura smooth between punctures. Propodeal lateral surface with minute, faint punctures separated by 2–3 times a puncture width, integument between smooth; basal area of propodeum glabrous. Metasoma faintly imbricate and impunctate.

Color, where evident, dark brown, without maculations. Wing membrane hyaline; veins strong and dark brown.

Pubescence generally whitish. Labrum with moderate-length, simple, erect setae widely scattered over surface. Clypeus with minute, suberect, simple setae restricted to lateral borders and short, simple, suberect, anteriorly-directed setae on dorsal-facing surface of clypeal protrusion. Face with sparse, suberect, minute, simple setae, such setae becoming slightly more dense in lower paraocular area near clypeal lateral border. Setae of vertex and gena as described for face. Postgena with short, simple, erect setae. Pubescence of pronotum as described for face except setae of dorsal surface restricted to posterior border. Mesoscutum with short, sparse, simple, erect setae evident through thin layer of Schimmel. Scutellum with erect, long (1–3 OD) setae on posterior third, setae each with several minute branches. Hypoepimeral area without setae; remainder of pleura with pubescence as described for face. Lateral surface of propodeum with pubescence as described for face; basal area of propodeum without setae. Inner surface of metafemur and metatrochanter without pubes-



Figs. 96–98. Head of holotype female of *Succinapis proboscidea,* new species. **96.** Frontal view. **97.** Oblique, lateral view. **98.** Dorsal view. Scale bar = 0.5 mm.

cence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate zone; corbicula bordered by long, minutely-plumose setae; metatarsus with simple, stout setae; six comb rows on inner surface of metabasitarsus. Metasomal terga with scattered, simple, short, appressed setae, sparse on central discs; sterna with scattered, simple, erect, slightly fuscous setae.

MATERIAL: Three specimens. **Holotype.** Female, worker caste, B-JH 96 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Succinapis proboscidea* Engel".

Paratype. Female, worker caste, B-JH 99 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Paratype, *Succinapis proboscidea* Engel".

Paratype. Female, worker caste, Nr. 10 (CSUL) labeled: "Paratype, *Succinapis proboscidea* Engel".

ETYMOLOGY: The specific epithet is derived from the Greek word *proboskidos,* referring to the trunk of an elephant, and is a reference to the structure of the large clypeal protrusion of this species.

Internal Phylogeny of *Succinapis*

The morphology of the clypeal protrusion suggests a hierarchy of relationship among the species of *Succinapis* (fig. 99). By comparison to other melikertine genera as outgroups it is possible to build a preliminary cladistic hypothesis for the three known *Succinapis* species. The presence of the clypeal protrusion is a unique apomorphy among the corbiculate Apinae and nicely serves to support the monophyly of the genus. The polarity of the different morphotypes of clypeal protrusions is impossible to determine in isolation from other characters as there is no corresponding structure in the outgroups. The apically bent clypeal protrusions of *S. micheneri* and *S. proboscidea* could be interpreted as plesiomorphic with *S. goeleti* and *S. micheneri* perhaps clustered on the basis of shortened protrusion and *S. goeleti* autapomorphic for a straight process, or if the polarity of the protrusion's size is removed, then our three-taxon statement collapses to a trichotomy. The same scenario of difficulties applies if the polarities are reversed for each of the discussed characters. Fortunately, the sculpturing of the mesepisternum provides some information that can be compared to the related melikertine genera and for polarizing the species in *Succinapis.* The mesepisternum in all species of *Melikertes* is smooth and impunctate. Within *Succinapis* smooth pleural integument is only found in *S. goeleti,* while both *S. micheneri* and *S. proboscidea* have punctured mesepisterna. It would therefore appear that *S. goeleti* is the most plesiomorphic species of the genus by comparison to *Melikertes.* This hierarchy polarizes the clypeal protrusion morphology (fig. 99). The shortened clypeal protrusion that does not project more than an antennal socket diameter above the antennal sockets observed in *S. goeleti* and *S. micheneri* is presumably plesiomorphic. The apical bend of the clypeal protrusion is an apomorphic feature uniting *S. micheneri* and *S. proboscidea,* while the greatly enlarged process is an autapomorphy of *S. proboscidea* (fig. 99).

Genus *Melikertes* Engel, status novus

Electrapis (*Melikertes*) Engel, 1998a: 95. Type species: *Electrapis* (*Melikertes*) *stilbonota* Engel, 1998a, original designation.

DIAGNOSIS: This genus is similar to *Succinapis* but lacks the basal clypeal protrusion.

DESCRIPTION: Malar space short, shorter than basal mandibular width. Epistomal sulcus forming obtuse angle or nearly linear (e.g., *M. stilbonotus*: fig. 100); clypeus without basal clypeal protrusion (fig. 100). F1 longer than F2; F2 equal to F3. Inner margins of compound eyes roughly parallel. Preoccipital ridge rounded or weakly carinate. Mesoscutal anterior border broadly rounded; tegula tear-drop shaped; scutellum not bulging, not projecting over metanotum (fig. 101). Basal area of propodeum nearly horizontal, not declivitous. Keirotrichiate field not elevated (fig. 102); metatibial spur serrate or minutely ciliate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae (fig. 102); metabasitarsus parallel-sided (fig. 102). Three submarginal cells (fig. 103). Metasomal terga not banded.

COMMENTS: I previously (Engel, 1998a) erroneously reported an absence of metatibial

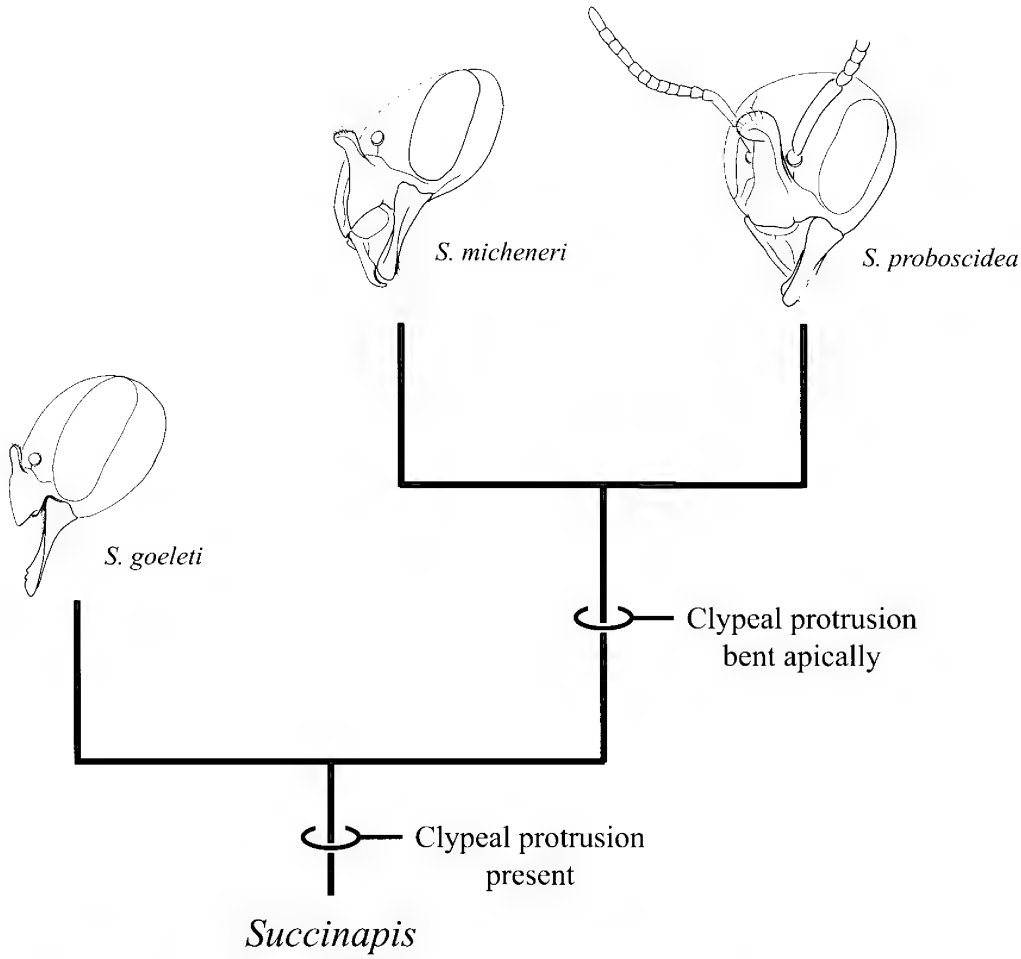


Fig. 99. Phylogeny of *Succinapis* based on morphology of the clypeal protrusion.

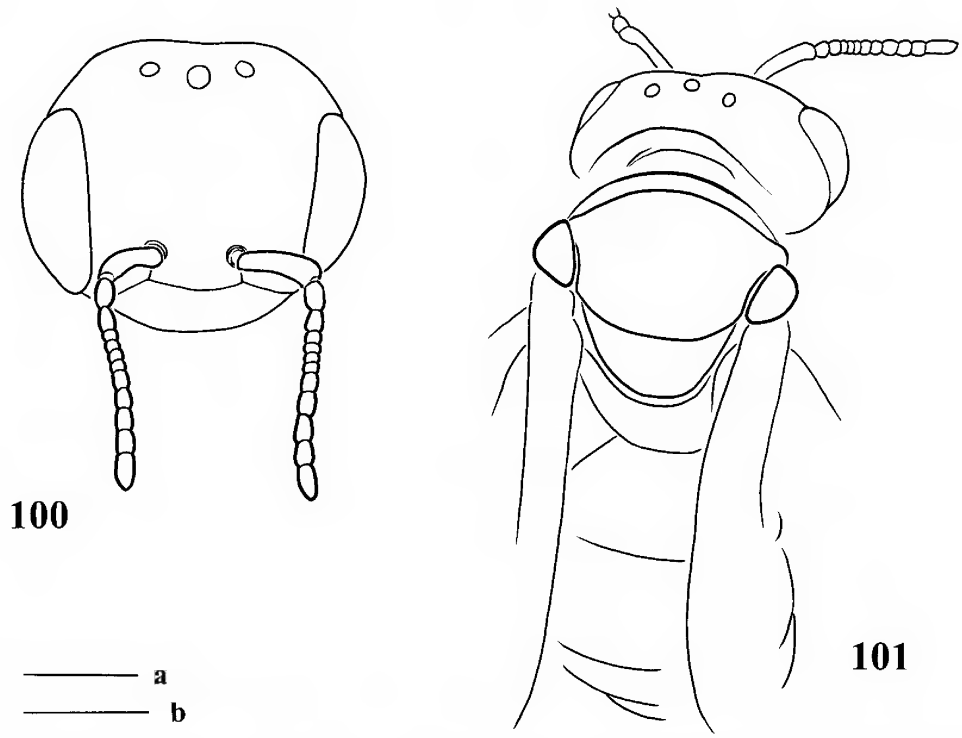
spurs for *Melikertes*. Subsequent study of the type material for *M. stilbonotus* as well as newly discovered material of other melikertine bees has revealed a single, reduced metatibial spur. This structure is difficult to observe in the holotype and paratype of *M. stilbonotus* but is distinctly present (fig. 102).

Key to Species of *Melikertes*

1. Tegula without posterior lamella, oval or teardrop shaped; body size small (ca. 3–4.5 mm) 2
– Tegula with short, posterior lamella; body size moderate (ca. 8 mm) .... *M. proavus* (Menge)
2. Apical margin of clypeus unmodified, straight, and flat as on remainder of clypeus ..... *M. stilbonotus* (Engel)
– Apical margin of clypeus strongly projecting outward from face with deep medial cleft, remainder of clypeus relatively flat .... *M. clypeatus,* n. sp.

Melikertes proavus (Menge), new combination

Apis proava Menge, 1856: 26.
Electrapis (*Roussyana*) *proava* (Menge); Zeuner and Manning, 1976: 236.
Trigona (*Roussyana*) *proava* (Menge); Kerr and Cunha, 1976: 39.



Figs. 100–101. Holotype female of *Melikertes stilbonotus* (Engel). **100.** Frontal view of head. **101.** Dorsal view. Scale bars = 0.5 mm (a = fig. 101; b = fig. 100).

Electrapis (*Melikertes*) *proava* (Menge); Engel, 1998a: 95.

DIAGNOSIS: This is the largest and least understood species of *Melikertes* (simply owing to the fact that the two specimens known are in poor condition by comparison to material of other species). The species is exceptional for its large size compared to other *Melikertes*.

DESCRIPTION: **Female.** Total body length 8.30 mm; forewing length 6.0 mm. Apical margin of clypeus straight, not bent apically. Intertegular distance 2.15 mm. Tegula with short, posterior lamella. Basal vein basad cu-a by two times vein width; 1m-cu bisecting second submarginal cell; 2rs-m distad 2m-cu; first submarginal cell only slightly shorter than second and third combined; second submarginal cell narrowed anteriorly, not very strongly so; length of anterior border of third submarginal cell half of that of posterior border, anterior border about as long as that of anterior border of second submarginal cell; six distal hamuli, arranged in a single, evenly spaced series.

Integument of head, mesosoma, and metasoma apparently smooth and impunctate except metanotum rugulose and sterna imbricate.

Coloration not well preserved, apparently dark brown to black and shining, without maculations. Wing membrane hyaline; veins strong and dark brown.

Pubescence generally pale. Setae of face and vertex widely scattered, simple, and short. Gena with simple, short, suberect setae very sparsely scattered; postgena with long, simple setae sparsely scattered over integument. Pronotal collar without pubescence; pronotal border with mesoscutum with short, simple setae; lateral surface with similar minute setae. Mesoscutum with scattered, minute setae, more sparsely scattered on central disc. Pubescence of scutellum as described

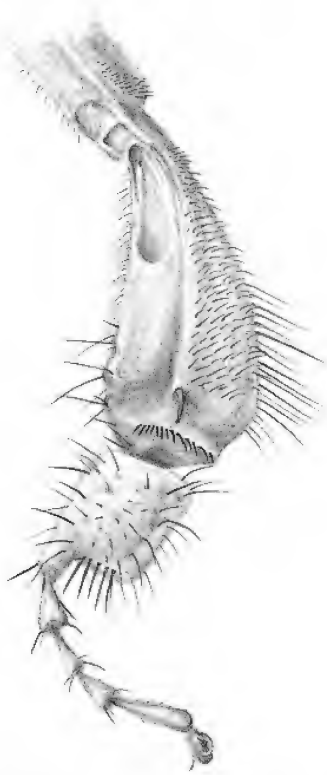


Fig. 102. Inner surface of metatibia and metatarsus of holotype female of *Melikertes stilbonotus* (Engel).

for mesoscutum. Hypoepimeral area without pubescence; remainder of mesepisternum with widely scattered, minute setae. Basal area and posterior surface of propodeum without pubescence. Inner surface of metafemur and metatrochanter without pubescence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate zone. T1 without pubescence on central disc, a few, simple setae on lateral borders; pubescence of T2–T6 as described for T1 except a few simple setae on posterolateral borders; sterna with sparse, simple, subappressed setae.

MATERIAL: Two specimens. **Neotype.** Female, worker caste, Nr. 13781 (BMNH) labeled: "No. 13781, Bee, Museum Stantien & Becker" // "515, Dr. R. Klebs, 92–14 [74?]" // "XII B781 [on the amber block]" // "*Electrapis proava* (Menge), Amber, East Prussia, Paralectotype, Transf. [transferred] from Zool. Dept. [Zoology Department], 15 Dec. [December] 1904, (In. 18757), 92–14 [74?]" // "Neotype, *Apis proava* Menge, 1856, desig. ICZN (M. S. Engel)". Formerly the paralectotype designated by Zeuner and Manning (1976: 236; see Comments below); designated as neotype by ICZN Opinion Nr. 1964 (ICZN, 2000). The amber piece is set into Canadian balsam and mounted onto a microscope slide.

Non-type. Female, worker caste, In. 43592 (BMNH) labeled: "In. 43592, E. proava, Lectotype" // "*M. proava*? (Menge), non-type, desig. ICZN (M. S. Engel)" // "*Melikertes proavus*? (Menge), det. M. S. Engel". Formerly lectotype; designation by Zeuner and Manning (1976: 236; see Comments below). This individual is assigned to *M. proavus* with great hesitation owing to its extremely poor condition. Zeuner and Manning (1976), who examined the specimen before it was damaged, considered it to be conspecific with the above specimen.

COMMENTS: The type designations of Zeuner and Manning (1976) have been suppressed owing to the poor condition of their chosen lectotype (Engel, 1999a; ICZN, 2000).

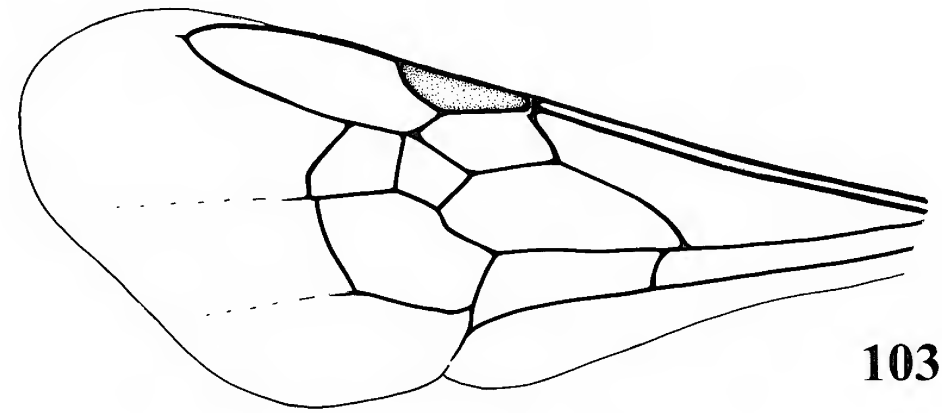
Melikertes stilbonotus (Engel), new combination

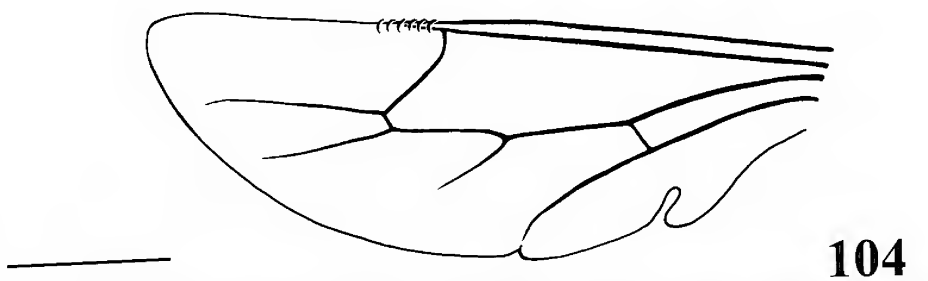
Figures 100–104

Electrapis (*Melikertes*) *stilbonota* Engel, 1998a: 95.

DIAGNOSIS: Refer to diagnosis for *M. clypeatus* (see below).

DESCRIPTION: **Female.** Total body length 3.76 mm; forewing length 3.00 mm. Head wider than long (length 1.12, width 1.32: measurements from paratype). Upper interorbital distance 0.86 mm; lower interorbital distance 0.82 mm (both metrics from paratype). Apical margin of clypeus straight, not bent apically. Intertegular distance 0.82 mm. Basal vein basad cu-a by two times vein width; 1m-cu bisecting second submarginal cell; 2rs-m distad 2m-cu by 1.5 times vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-tenth that of posterior border (i.e., second submar-





Figs. 103–104. Wings of holotype female of *Melikertes stilbonotus* (Engel). **103.** Forewing. **104.** Hind wing. Scale bar = 0.5 mm.

ginal cell strongly narrowed anteriorly); length of anterior border of third submarginal cell half of that of posterior border, just over three times length of anterior border of second submarginal cell; six distal hamuli, arranged in a single, evenly spaced series; cu-a of hind wing orthogonal to M+Cu.

Integument of head, mesosoma, and metasoma smooth and impunctate except metanotum rugulose. S3–6 weakly and sparsely nodulate, integument between smooth.

Coloration not well preserved, apparently dark brown to black and shining, without maculations. Wing membrane hyaline; veins strong and dark brown.

Pubescence generally pale. Setae of face widely scattered, simple, and short; such hairs becoming gradually longer toward vertex. Gena with simple, short, suberect setae; postgena with long, simple setae sparsely scattered over integument. Pronotal collar without pubescence; pronotal border with mesoscutum with short, simple setae; lateral surface with similar minute setae, such setae appressed but not obscuring integument. Mesoscutum with scattered, simple setae, more sparsely scattered and shorter on central disc, those setae on anterolateral borders with a few short branches. Pubescence of scutellum as described for mesoscutum except longer and restricted to posterior border. Metanotum with dense, minute, simple setae, not obscuring integument. Hypoepimeral area without pubescence; remainder of mesepisternum with scattered, simple setae, such setae gradually become longer ventrally; central disc, however, without pubescence. Basal area and posterior surface of propodeum without pubescence; lateral surface with scattered, long, simple setae intermixed with shorter, ap-

pressed setae, such setae partially obscuring integument. Pubescence of legs generally simple and scattered except inner surfaces of mesotrochanter and mesofemur without pubescence and outer surface of mesotibia with dense, branched setae; inner surface of metafemur and metatrochanter without pubescence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate zone; eight comb rows on inner surface of metabasitarsus, each composed of stiff, elongate, simple setae; outer surface with scattered, long, simple setae. T1 without pubescence on central disc, a few, simple setae on lateral borders; pubescence of T2 as described for T1 except a few simple setae on posterolateral borders; T3–6 with simple setae longer than those of T1–2, sparsely scattered over central disc, more concentrated on lateral margins; sterna with sparsely scattered, simple setae.

MATERIAL: Five specimens. **Holotype.** Female, worker caste, In. 17778 (BMNH). The specimen bears labels reading "Holotype, *Electrapis stilbonota,* desig. M. S. Engel [red label]" // "Amber Inclusa, Hymenoptera, In. 17778, Samland, No. 67 [white label]". Amber piece preserved in Canadian balsam on a slide mount.

Paratype. Female, worker caste, In. 17778 (BMNH); same block of amber as holotype. Paratype total body length 3.72 mm; forewing length 3.16 mm. Refer to Engel (1998a) for more measurements.

Non-type. Female, worker caste, B-JH 76 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Melikertes stilbonotus* (Engel), det. M. S. Engel".

Non-type. Female, worker caste, B-JH 82 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "*Melikertes stilbonotus* (Engel), det. M. S. Engel".

Non-type. Female, worker caste, Nr. 63 (CJDL) labeled: "Nr. 63" // "*Melikertes stilbonotus* (Engel), det. M. S. Engel".

***Melikertes clypeatus*,** new species

Plate 7a

DIAGNOSIS: This species is most similar to *M. stilbonotus,* the two species looking remarkably similar. *Melikertes clypeatus,* however, is immediately recognizable by the peculiar modification of the clypeal apical margin that is strongly flexed forward below the level of the lower tangent of the compound eyes. Moreover, the projecting portion of the clypeal apical margin possesses a strong medial cleft.

DESCRIPTION: **Female.** Total body length 3.10 mm; forewing length 2.65 mm. Head wider than long (length 1.02 mm, width 1.22 mm). Upper interorbital distance 0.83 mm; lower interorbital distance 0.75 mm. Interocellar distance 0.23 mm; ocellocular distance 0.28 mm; median to lateral ocellus 0.07 mm. Apical margin of clypeus strongly bent apically, with distinct medial cleft. Intertegular distance 0.83 mm. Basal vein basad cu-a by two times vein width; 1rs-m distad 1m-cu by six times vein width; 2rs-m distad 2m-cu by three times vein width; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-third that of posterior border; length of anterior border of third submarginal cell half of that of posterior border, twice length of anterior border of second submarginal cell; five distal hamuli, arranged in a single, evenly spaced series.

Integument of head, mesosoma, and metasoma smooth and impunctate.

Coloration not preserved. Wing membrane hyaline; veins strong and brown.

Pubescence generally pale. Setae of face sparse, simple, suberect, and short, although such setae becoming erect on vertex. Mesoscutum with sparse, simple, short setae. Pubescence of scutellum as described for mesoscutum except longer on posterior border. Pleura with sparse, simple, short setae. Pubescence of legs generally simple and scattered except inner surfaces of mesotrochanter and mesofemur without pubescence and outer surface of mesotibia with dense, branched setae; inner surface of metafemur and metatrochanter without pubescence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate zone; comb rows on inner surface of metabasitarsus, each composed of stiff, elongate, simple setae; outer surface with scattered, long, simple setae. Terga and sterna with exceedingly sparse, minute, simple, appressed or subappressed setae.

MATERIAL: **Holotype.** Female, worker caste, B-JH 77 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Melikertes clypeatus* Engel". The only known specimen has a great deal of Schimmel on the mesosoma that entirely obscures the propodeum and metanotum. The scutellum, mesoscutum, tegula, and pleura can be seen with some difficulty. The posterior portion of the head is also covered with some Schimmel, as are lateral portions of T1.

ETYMOLOGY: The specific epithet is a reference to the modified apical margin of the clypeus.

***Melissites*, new genus**

TYPE SPECIES: *Melissites trigona* Engel, new species.

DIAGNOSIS: See Diagnosis for *Roussyana* (below).

DESCRIPTION: Malar space short, shorter than basal mandibular width (fig. 105). Epistomal sulcus forming obtuse angle (fig. 105); clypeus without basal clypeal protrusion. F1 longer than F2; F2 shorter than F3. Compound eyes strongly converging below and emarginate (fig. 105). Preoccipital ridge rounded. Mesoscutal anterior border broadly rounded; tegula oval; scutellum bulging, projecting over metanotum and basal area of propodeum. Basal area of propodeum declivitous. Keirotrichiate field not elevated (fig. 107); metatibial spur ciliate; auricular basket sparse, setae short (fig. 106); rastellum strong and formed of stiff setae; lateral margins of metabasitarsus converging toward apex (figs. 106, 107). Three submarginal cells; anterior border of second submarginal cell as long as r-rs (fig. 109). Metasomal terga banded.

ETYMOLOGY: The new genus-group name is a combination of *melissa* (Greek, meaning "bee") and the suffix *-ites* (Greek, meaning "nature of" or "likeness", a common suffix for fossil genera). The name is feminine.

***Melissites trigona*, new species**

Figures 105–110

Plate 6d

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 4.22 mm; forewing length 4.00 mm. Head wider than long (length 1.25 mm, width 1.53 mm). Upper interorbital distance 0.97 mm; lower interorbital distance 0.73 mm. Interocellar distance 0.37 mm; ocellocular distance 0.22 mm; median to lateral ocellus 0.12 mm. Intertegular distance 1.00 mm. Basal vein confluent with cu-a; 1rs-m distad 1m-cu by eight times vein width; 2rs-m distad 2m-cu by 1.5 times vein width; first submarginal cell shorter than combined lengths of second and third submarginal cells; length of posterior border of second submarginal cell slightly less than twice anterior border; length of anterior border of third submarginal cell three-quarters that of posterior border, 1.25 times length of anterior border of second submarginal cell; six distal hamuli arranged in a single, evenly spaced series (fig. 110).

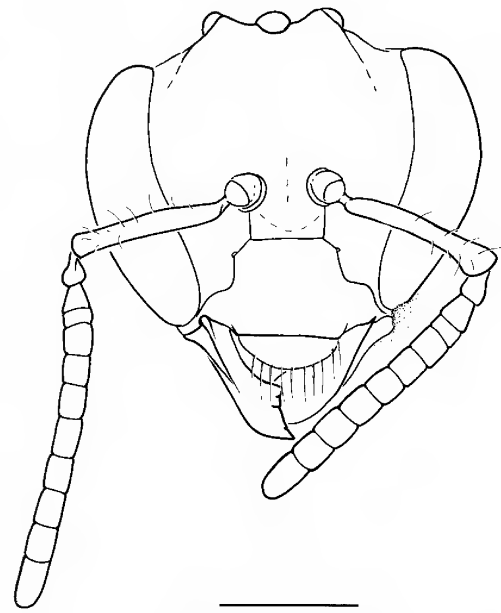
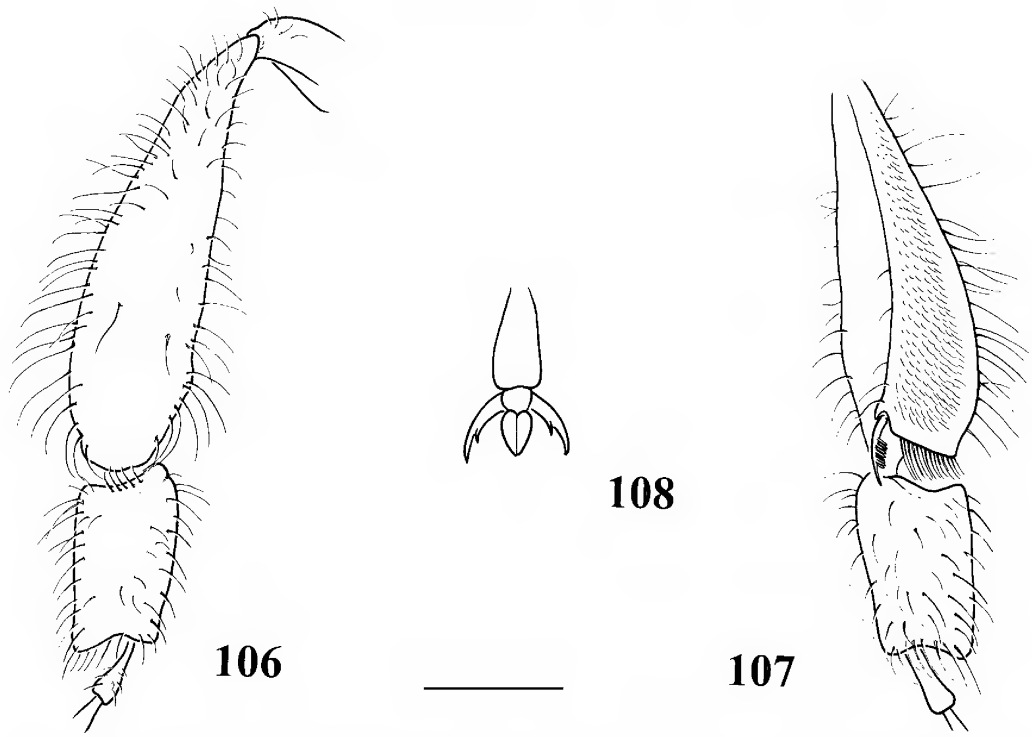


Fig. 105. Frontal view of holotype female head of *Melissites trigona,* new species. Scale bar = 0.5 mm.

Integument of head and mesosoma smooth and impunctate. Terga and sterna imbricate and impunctate.

Head and mesosoma black. Antennae, legs, and metasoma dark brown except apical margins of terga light brown to pale yellow.



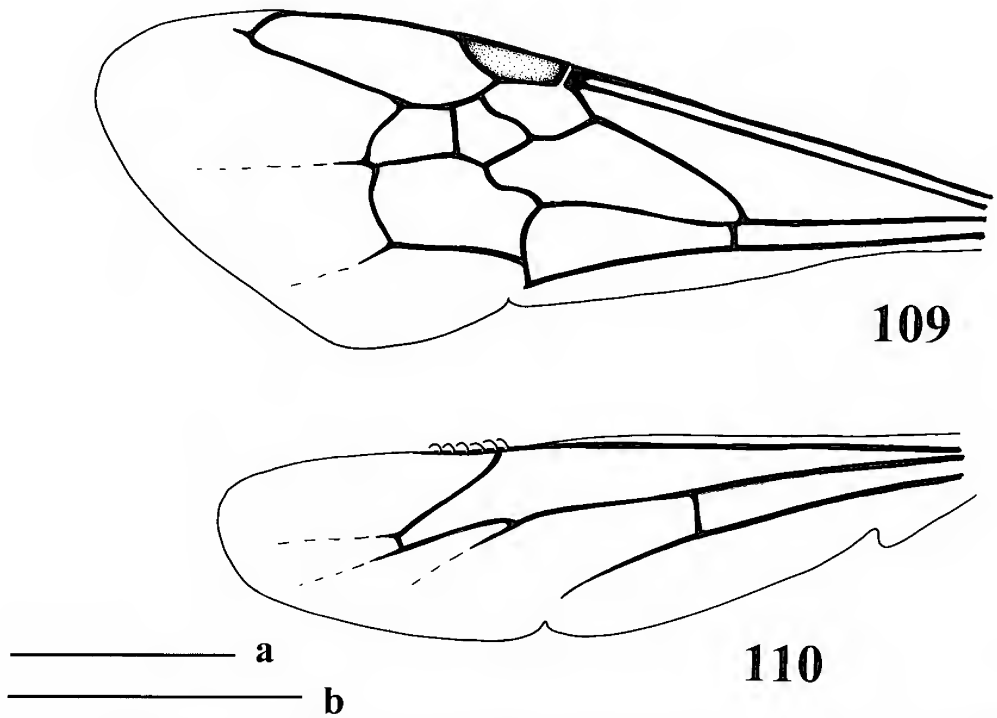
Figs. 106–108. Leg structures of holotype female of *Melissites trigona,* new species. **106.** Outer surface of metatibia and metabasitarsus. **107.** Inner surface of metatibia and metabasitarsus. **108.** Claw and arolium. Scale bar = 0.5 mm (figs. 106, 107); 0.25 mm (fig. 108).

Wing membrane hyaline; veins strong and dark brown.

Pubescence lightly infuscated. Setae of face widely scattered, simple, and short; such setae longer on vertex. Gena with simple, short, appressed setae; postgena with long, simple setae sparsely scattered. Mesoscutum with sparse, simple setae, more sparsely scattered and shorter on central disc. Pubescence of scutellum as described for mesoscutum except two or more times longer, plumose, and dense on posterior half. Metanotum without pubescence. Hypoepimeral area without pubescence; remainder of mesepisternum and metepisternum with scattered, simple, long setae. Basal area and posterior surface of propodeum without pubescence; lateral surface with scattered, minute, suberect, simple setae. Pubescence of legs generally simple and scattered except inner surfaces of mesotrochanter and mesofemur without pubescence and outer surface of mesotibia with dense, branched setae; inner surface of metafemur and metatrochanter without pubescence except apical quarter of metafemur with dense field of keirotrichiae; inner surface of metatibia with keirotrichiate zone; corbicular setae simple; seven comb rows on inner surface of metabasitarsus, each composed of stiff, elongate, simple setae; outer surface with scattered, long, simple setae. Terga and sterna with short, simple, sparse setae.

MATERIAL: One specimen. **Holotype.** Female, worker caste, B-JH 102 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Melissites trigona* Engel".

ETYMOLOGY: The specific epithet is taken (as a noun in apposition) from the genus-group name *Trigona* (Meliponini) and is a



Figs. 109–110. Wings of holotype female of *Melissites trigona,* new species. **109.** Forewing. **110.** Hind wing. Scale bars = 1 mm (a = fig. 109; b = fig. 110).

reference to the overall, superficial resemblance of this species to some stingless bees.

Genus *Roussyana* Manning, status novus

Electrapis (*Roussyana*) Manning, 1960: 306. Type species: *Apis palmnickenensis* Roussy, 1937, original designation. Zeuner and Manning, 1976: 233.
Russyana Petrov, 1992: 361. *Lapsus calami.*

DIAGNOSIS: *Roussyana* most closely resembles *Melissites*; both genera have the distinctive banding of the metasoma owing to the apical margins of the terga being very pale brown in comparison to the remainder of the terga, which are dark brown. The genus can be separated from *Melissites* by the strongly narrowed second submarginal cell, basal vein basal to cu-a, and the approximately parallel compound eyes.

DESCRIPTION: Malar space short, shorter than basal mandibular width. Epistomal sulcus forming obtuse angle; clypeus without basal clypeal protrusion. F1 longer than F2; F2 equal to F3. Inner margins of compound eyes roughly parallel. Preoccipital ridge rounded. Mesoscutal anterior border broadly rounded; tegula oval; scutellum bulging, projecting over metanotum and basal area of propodeum. Basal area of propodeum declivitous. Keirotrichiate field not elevated; metatibial spur serrate; auricular basket sparse, setae short; rastellum strong and formed of stiff setae; lateral margins of metabasitarsus converging toward apex. Three submarginal cells; anterior border of second submarginal cell much shorter than r-rs. Metasomal terga banded.

Roussyana palmnickenensis (Roussy)

Apis palmnickenensis Roussy, 1937: 66.
Electrapis (*Roussyana*) *palmnickenensis* (Roussy); Manning, 1960: 306. Zeuner and Manning, 1976: 233 [misidentification: see *Succinapis micheneri,* above]

Electrapis minuta Kelner-Pillault, 1970a: 16. NEW SYNONYMY.

Trigona (*Roussyana*) *palmnickenensis* (Roussy); Kerr and Cunha, 1976: 39.

Roussyana palmuickenensis Petrov, 1992: 361. *Lapsus calami.*

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 3.08 mm; forewing length 2.3 mm. Head longer than wide (length 0.93 mm, width 0.88 mm). Mandible with a single small tooth on upper one-fifth of apical margin. Intertegular distance 0.82 mm. Basal vein basad cu-a by two times vein width; 1rs-m distad 1m-cu by seven times vein width; 2rs-m distad 2m-cu by two times vein width; first submarginal cell shorter than combined lengths of second and third submarginal cells; second submarginal cell strongly narrowed anteriorly, anterior border shorter than r-rs; anterior border of third submarginal cell approximately nine times longer than anterior border of second submarginal cell; six distal hamuli arranged in a single, evenly spaced series.

Head and mesosoma smooth and impunctate except corbicula finely imbricate. Terga and sterna finely and faintly imbricate except lighter apical margins of terga glabrous.

Head and mesosoma black. Antennae, legs, tegulae, and metasoma dark brown except apical margins of terga light brown.

Pubescence generally pale. Labrum with several, long, simple setae widely scattered. Setae of face widely scattered, simple, and short, although setae becoming slightly longer on vertex. Mesoscutum with scattered, long, simple setae. Pubescence of scutellum as described for mesoscutum except somewhat longer. Metanotum without pubescence. Hypoepimeral area without pubescence; remainder of mesepisternum with scattered, simple setae, although particularly sparse on central disc; setae slightly longer ventrally. Basal area of propodeum without pubescence. Pubescence of legs generally simple and scattered except inner surfaces of mesotrochanter and mesofemur without pubescence and outer surface of mesotibia with dense, branched setae; inner surface of metafemur and metatrochanter without pubescence; inner surface of metatibia with keirotrichiate zone; distinct comb rows on inner surface of metabasitarsus, each composed of stiff, elongate, simple setae; outer surface with scattered, long, simple setae. T1–5 with sparse, minute, suberect, simple setae; T6 with numerous, short, simple setae uniformly covering surface; sterna with sparsely scattered, short, simple setae and with dense, subapical rows of long setae.

MATERIAL: Three specimens. **Neotype (*palmnickenensis*; here designated).** Female, worker caste, NB.I.1945 [Berendt Collection] (ZMHB) labeled: "Neotype, *Apis palmnickenensis* Roussy, desig. M. S. Engel" // "50a" [Berendt handwriting] // "NB.I.1945". The types for Roussy's species were in his private collection. A diligent search for their whereabouts failed to locate them. I have thus here designated a neotype for the species. The limited description Roussy (1937) presented for the species, however, best agrees to Kelner-Pillault's specimens among all of the corbiculate bees in Baltic amber. I, therefore, believe Roussy's and Kelner-Pillault's specimens to be conspecific and have chosen the most completely preserved of the two individuals in the piece to serve as the neotype for *Apis palmnickenensis* Roussy as well as the lectotype for *Electrapis minuta* Kelner-Pillault. The two paralectotype individuals (designated below) are clustered together on one end of the piece, while the neotype/lectotype is alone on the opposite end.

Lectotype (*minuta*; here designated). Female, worker caste, NB.I.1945 (ZMHB) labeled: "Lectotype, *Electrapis minuta* Kelner-Pillault, desig. M. S. Engel" // "*Electrapis minuta* S.K.P., syntypes, S. Kelner-Pillault, det." [Kelner-Pillault handwriting] // "*Roussyana minuta* (Kelner-Pillault), det. M. S. Engel, 1999". Since this is the same specimen designated above as the neotype for *A. palmnickenensis,* the remaining labels are identical to those listed above for *A. palmnickenensis* (refer to preceding paragraph).

Paralectotypes (*minuta*; here designated). Two females, worker caste, NB.I.1945 (ZMHB): these specimens are in the same amber block as the lectotype and bear the same labels. They are distinguished from the lectotype by the poorer state of preservation, both are heavily covered in Schimmel and surrounded by numerous small fracture planes.

COMMENTS: The specimen figured as a non-type of *Roussyana palmnickenensis* by Zeuner and Manning (1976: their pl. 3 as *Electrapis palmnickenensis*) is not actually a specimen of *Roussyana.* The specimen is in GPUH and upon examination it is actually *S. micheneri.* The specimen lacks the defining features of not only the species but also the genus. Moreover, the specimen has a distinct clypeal protrusion (a character of *Succinapis*) and sparse mesoscutal setae. A thin layer of pollen and mold on the specimen was apparently interpreted as copious pubescence by Zeuner and Manning. The description they presented for *R. palmnickenensis,* therefore, does not apply to this species.

Kelner-Pillault (1970a) designated the two specimens discussed above as syntypes but did not select one to be the name-bearing type. I have, therefore, in the interest of nomenclatural stability, selected a lectotype and paralectotype from her syntypes. Kelner-Pillault (1970a) enigmatically figured the hind wing without a jugal lobe, which is not only present but deeply incised and visible in the specimens.

Tribe MELIPONINI Lepeletier de Saint Fargeau

Meliponites Lepeletier de Saint Fargeau, 1836: 407. Type genus: *Melipona* Illiger, 1806.
Trigonini Moure, 1946: 611. Type genus: *Trigona* Jurine, 1807.
Lestrimelittini Moure, 1946: 611. Type genus: *Lestrimelitta* Friese, 1903.

DIAGNOSIS: Among living taxa the Meliponini are allied to the honey bees (tribe Apini); both tribes share the complete loss of metatibial spurs and outer mandibular grooves and possess a jugal lobe in the hind wing. The meliponines differ from Apini by the absence of an auricle, absence of an inner tooth on the claw, the reduced forewing venation, and the reduction of the sting, among other characters. Numerous ethological traits similarly serve to differentiate the tribes (reviewed by Michener, 1990: as subfamilies). Among the fossil taxa meliponines most closely resemble the tribe Melikertini but differ notably by the aforementioned characters as well as the complete loss of metatibial spurs (melikertines retain a single metatibial spur).

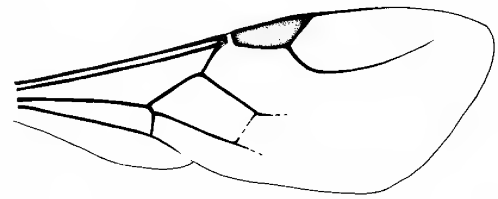


Fig. 111. Forewing of holotype female of *Kelneriapis eocenica* (Kelner-Pillault). Scale bar = 0.5 mm.

DESCRIPTION: Minute to moderate size (ca. 1.5–13 mm long), sparsely to moderately pubescent bees. Mandible without outer mandibular grooves. Labral width three to four times length. Clypeus variously produced, typically gently convex and not protuberant in profile. Compound eyes typically bare. Supraälar carina absent; scutellum broadly rounded posteriorly and variously produced (i.e., ranging from projecting over metanotum and propodeum to not projecting at all: e.g., see Michener, 1990). Claws of female simple (e.g., fig. 115); arolium strong and present; metatibial spurs absent; malus of strigilis without anterior velum; metabasitarsus without auricle; metatibia with penicillum (e.g., fig. 114). Distal venation of forewing weakened (e.g., figs. 111, 113); marginal cell apex typically open (e.g., figs. 111, 113); pterostigma present, moderate to large in size, much longer than prestigma, r-rs arising near midpoint, margin within marginal cell convex; 1m-cu, when present, angled; hind wing with distinct jugal lobe, lobe broadly and deeply incised; hamuli reduced; wing membrane without alar papillae. Sting reduced.

COMMENTS: The tribe Meliponini contains the familiar stingless bees. The group is today worldwide in the tropics, with a particularly high diversity in the neotropics. Michener (2000a) recognized 23 Recent genera and subgenera worldwide. Although no meliponines today occur in Europe, at least two species were present in the middle Eocene fauna of this region. Both seem closely allied to Recent sub-Saharan African genera.

Key to Genera of Meliponini in Baltic Amber

1. Apical bend in M (at point where vein would meet 1m-cu) present (fig. 111); antennal sockets at least one antennal socket diameter above basal clypeal margin; posterior corner of corbicula weakly rounded; scutellum projecting over metanotum and propodeum; basal area of propodeum shorter than scutellum and declivitous .... *Kelneriapis* Sakagami
– Apical bend in M (at point where vein would meet 1m-cu) absent (fig. 113); antennal sockets less than one antennal socket diameter from basal clypeal margin (fig. 112); posterior corner of corbicula distinctly pointed (fig. 114); scutellum not projecting over metanotum; basal area of propodeum horiztonal and as long as scutellum ..... *Liotrigonopsis,* n. gen.

Genus *Kelneriapis* Sakagami

Tetragonula (*Kelneriapis*) Sakagami, 1978: 232. Type species: *Hypotrigona eocenica* Kelner-Pillault, 1969a, monobasic. Michener, 1990: 106 [as a genus].

Kelnermelia Moure *In* Moure and Camargo, 1978: 565. Type species: *Hypotrigona eocenica* Kelner-Pillault, 1969a, monobasic and original designation, isotypic with *Kelneriapis* Sakagami, 1978.

DIAGNOSIS: This genus differs from the only other Baltic amber meliponine genus, *Liotrigonopsis,* by the separation of the antennal sockets from the basal margin of the clypeus more than 1 OD, the rounded apical corner of the metatibia, the scutellum projecting over the metanotum and propodeum, and the strongly declivitous and shortened basal area of the propodeum. Among living genera *Kelneriapis* is most similar to, and perhaps sister to, *Hypotrigona* from Africa; both genera have the posterior apical corner of the metatibia rounded, although slightly less so in *Kelneriapis*. *Kelneriapis* differs, however, by the scutellum that projects over the metanotum and propodeum, the absence of mandibular dentition, and the shortened and declivitous propodeum.

DESCRIPTION: Mandible without dentition. Malar space shorter than basal mandibular width. Antennal sockets set above base of clypeus by more than an antennal socket diameter. F1 approximately equal in length to pedicel; F1 shorter than F2; F2 approximately equal in length to F3; flagellomeres with numerous, minute sensillar plates. Inner margin of compound eyes straight, eyes apparently parallel (not converging below). Preoccipital area rounded. Anterior border of mesoscutum broadly rounded; tegula oval; scutellum strongly projecting over metanotum and propodeum, without medioapical V-shaped notch, apical margin rounded. Basal area of propodeum much shorter than scutellum, strongly declivitous. Corbicula only weakly concave along apical third of metatibia; posterior angle of corbicula angled but not sharply (intermediate between *Hypotrigona* and *Liotrigona*); inner surface of metatibia with narrow keirotrichiate field, keirotrichiate field weakly elevated, bordered by broad, weakly depressed zone (as in *Hypotrigona*); inner surface of metabasitarsus without basal sericeous area. Forewing with distal bend at point where nebulous 1m-cu meets M present (fig. 111); no indication of submarginal cells (not even by nebulous veins); marginal cell apex open; hind wing difficult to see, without closed cells.

COMMENTS: The authorship of the name *Kelnermelia* was indicated as "Moure and Camargo" by Michener (1990, 1997); however, the name is attributed solely to Padre Moure in the original publication.

Unlike the description by Kelner-Pillault (1970b), which suggests that the specimen was a male (i.e., that there was no corbicula, 13 antennomeres, absence of penicillum), the specimen on which her description was based (labeled in her own hand as the holotype and matching the photograph she presented) is in fact a female with a corbicula, 12 antennomeres, and a penicillum.

Kelneriapis eocenica (Kelner-Pillault), new combination

Figure 111

Plate 7e

Hypotrigona eocenica Kelner-Pillault, 1969a: 87.

Trigona (*Hypotrigona*) *eocenica* (Kelner-Pillault); Kelner-Pillault, 1970b: 437.

Tetragonula (*Kelneriapis*) *eocenica* (Kelner-Pillault); Sakagami, 1978: 232.

Kelnermelia eocenica (Kelner-Pillault); Moure and Camargo, 1978: 565.

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 3.1 mm; forewing length 2.24 mm. Head wider than long (length 1.21 mm, width 1.24 mm). Interocellar distance 0.22 mm; ocellocular distance 0.17 mm; median to lateral ocellus 0.07 mm. Labrum much broader than long, apical margin straight. Glossa relatively short; flabellum minute; setae of labial palp segments identical to that described for *Liotrigona mahafalya* Brooks and Michener (Michener, 1990: his fig. 61). Scape relatively straight; flagellum with 10 flagellomeres (original description by Kelner-Pillault is in error). Forewings with identical venation (original description by Kelner-Pillault is in error by mentioning they are different!); basal vein basad cu-a crossvein.

Mandible smooth and impunctate, without outer grooves. Labrum, clypeus, supraclypeal area, face, vertex, and gena smooth and impunctate. Pronotum smooth and impunctate; mesoscutum smooth with a few, faint, small punctures separated by five times a puncture width or more; tegula and scutellum smooth and impunctate; metanotum apparently finely imbricate; pleura smooth and impunctate. Corbicula and outer surface of metabasitarsus finely imbricate. Basal area of propodeum glabrous (lateral and posterior surfaces not visible). Metasoma finely and faintly imbricate.

Head and mesosoma (where preserved) dark brown to black, without maculations. Legs dark brown. Wing membrane hyaline; veins light brown. Metasoma apparently dark brown.

Pubescence generally white. Mandible with widely scattered, minute, subappressed, simple setae. Labrum with minute, simple, subappressed setae evenly scattered over surface. Clypeus, supraclypeal area, and face to slightly above level of antennal sockets as described for labrum. Face above level of antennal sockets with setae as on clypeus but noticeably more sparse, erect, and intermixed with simple, erect, slightly longer setae; such erect setae also on vertex but disappearing on gena where pubescence is as described for clypeus. Mesoscutum with widely scattered, short, simple setae, setae becoming more dense toward anterolateral corners; tegula with scattered, minute, erect setae restricted to inner margin; scutellum as described for mesoscutum except setae slightly longer, setae noticeably more dense along posterior margin and slightly longer; metanotum and basal area of propodeum without pubescence. Corbicula bordered by long, simple setae; apex with penicillum; outer surface of metabasitarsus without pubescence, laterally with short, stiff, simple setae, inner surface with stiff comb rows. Metasoma with sparse, minute, simple, subappressed setae.

MATERIAL: One specimen. **Holotype.** Female, worker caste, MB.I.1946 (ZMHB) labeled: "15 [old Berendt collection number]" // "Holotyp [sic], Paläontologisches Museum Berlin, *Trigona* (*Hypotrigona*) *eocenica* Kelner-Pillault, 1970, Baltischer Bernstein" // "Holotype, *Trigona eocenica* Kelner-Pillault" // "*Hypotrigona eocenica* S.K.P., Holotype, S. Kelner-Pillault det.[in Kelner-Pillault's handwriting]".

COMMENTS: Although Kelner-Pillault's 1970 paper (1970b) is commonly cited as the original proposal of the species, the name was apparently made available by Kelner-Pillault a year earlier (1969a), where a one-sentence diagnosis is presented to separate the species from extant *Hypotrigona*; the name is given as "*Hypotrigona eocenica* n. sp.", and two figures are provided to distinguish the fossil from living meliponines. Although meeting abstracts are excluded from availability (ICZN, 1999b: Art. 9.9), published proceedings [as is the case for Kelner-Pillault (1969a)] are available. I therefore consider the name as having been made available in 1969 rather than 1970, and that the original combination was *Hypotrigona eocenica* rather than *Trigona* (*Hypotrigona*) *eocenica.*

Although Michener (1990) was the first to use *Kelneriapis* at the generic level (Sakagami treated this group as a subgenus of *Tetragonula*), he did not make the associated taxonomic combination for the type species and I have therefore considered my usage above to be a new combination.

***Liotrigonopsis*, new genus**

TYPE SPECIES: *Liotrigonopsis rozeni* Engel, new species.

DIAGNOSIS: In keys to the genera of Meliponini this group runs to the African and

Malagasy genus *Liotrigona* Moure (1961). This fossil differs, however, in the following generic characteristics: antennae inserted low on face (separated from clypeus by less than 1 OD) and not far above lower tangent of compound eyes as well as vein M without apical bend among other, more trivial, features. *Liotrigonopsis* can be separated from *Kelneriapis,* also in Baltic amber, by the characters presented above in the Diagnosis for *Kelneriapis.*

DESCRIPTION: Malar space shorter than basal mandibular width (fig. 112). Antennal sockets set near base of clypeus, separated by less than an antennal socket diameter (fig. 112). F1 approximately equal in length to F2; F2 approximately equal in length to F3; flagellomeres with numerous, minute sensillar plates. Preoccipital area rounded. Anterior border of mesoscutum broadly rounded; tegula oval; scutellum clearly not projecting over metanotum, without medioapical V-shaped notch, apical margin rounded. Basal area of propodeum as long as scutellum, horizontal. Posterior angle of corbicula sharply angled (as in *Liotrigona*) (fig. 114); inner surface of metatibia with narrow keirotrichiate field, keirotrichiate field not elevated, bordered by broad, glabrous zone; inner surface of metabasitarsus without basal sericeous area. Forewing without distal bend at point where 1m-cu would meet M (fig. 113); without indication of submarginal cells (fig. 113); marginal cell apex open; hind wing difficult to see, apparently without closed cells.

ETYMOLOGY: The new genus-group name is a combination of *Liotrigona* and the suffix *-opsis* (Greek, meaning "appearing like"). The name is a reference to the similarity between the fossil and *Liotrigona,* a genus of African and Malagasy stingless bees. The name is feminine.

***Liotrigonopsis rozeni*, new species**

Figures 112–115

Plate 7f

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Total body length 3.37 mm; forewing length 2.8 mm. Head length 0.87 mm (width indeterminate from specimen). Basal vein distad cu-a by three times vein width; minute basal stub of first abcissa of Rs after separation from M present, M terminating shortly thereafter without apical bend.

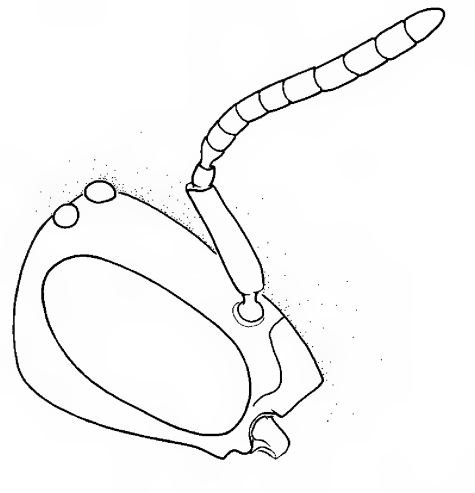


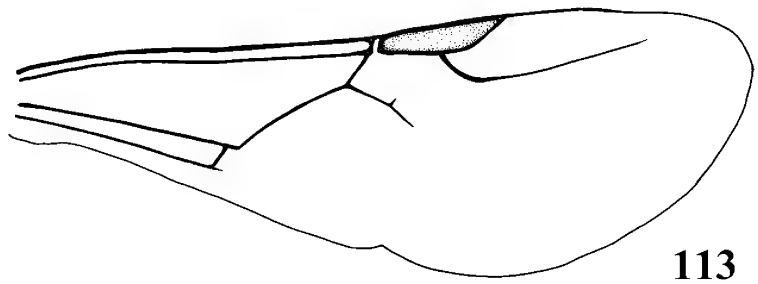
Fig. 112. Right lateral view of head of holotype female of *Liotrigonopsis rozeni,* new species. Scale bar = 0.5 mm.

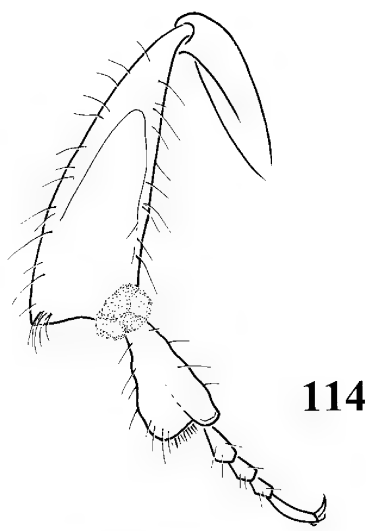
Integument of head, mesosoma, and legs smooth and impunctate. Terga and sterna finely imbricate and impunctate.

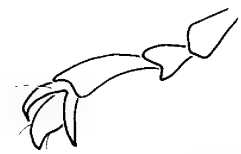
Head and mesosoma dark brown except scape light brown (remainder of antenna dark brown). Legs and metasoma light brown or ferruginous. Wing membrane hyaline; veins, when present, light brown.

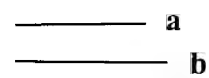
Pubesence golden, sparse, and simple. Setae not apparent on head. Mesosoma with sparse, simple, short, erect setae. Setae of legs simple and scattered; inner surface of metatibia densely covered by keirotrichiae except narrow (ca. 0.75 OD) glabrous posterior border; rastellar bristles of moderate length, tapering at apices, not flattened. Terga with exceedingly sparse, short, suberect setae; setae of sterna sparse, restricted to apical thirds, and moderately long.

MATERIAL: One specimen. **Holotype.** Female, worker caste, B-JH 79 (AMNH) labeled: "Baltic amber: Eocene, Kaliningrad, Yantarny" // "Holotype, *Liotrigonopsis rozeni* Engel." The specimen is partially preserved along the edge of the amber piece with the left half of the head and left anterior portion of the mesosoma missing. Enough of









Figs. 113–115. Mesosomal structures of *Liotrigonopsis rozeni,* new species. **113.** Forewing. **114.** Outer surface of metatibia and metatarsus. **115.** Metadistitarsus, claw, and arolium. Scale bars = 0.5 mm (a: for fig. 113) (b: for fig. 114); 0.25 mm (b: for fig. 115).

the specimen is preserved to allow for not only identification but for meaningful comparison to living species.

ETYMOLOGY: The specific epithet is a patronymic honoring Dr. Jerome G. Rozen, Jr. for his friendship and support of my studies on bees.

APOIDEA INCERTAE SEDIS

Genus and Species Indeterminate

The following specimens are too poorly preserved to allow identification below the level of family. I have listed them here simply as a record of the families and for the total number of individual bees recognized in Baltic amber.

APIDAE gen. et sp. indet.: **One female,** MB.I.1938 (ZMHB) labeled: "Museum für Naturkunde Berlin, Paläontologisches Museum, Inv. Nr. MB.I.1938 (No. 53)" // "53" // "Apidae indet., det. M. S. Engel". **One female,** Nr. 2616 (CCGG) labeled: "Nr. 2616" // "Apidae indet., det. M. S. Engel".

MEGACHILIDAE gen. et sp. indet.: **One**

female, Nr. 8 (CSUL) labeled: "Megachilidae indet., det. M. S. Engel".

Missing Taxa of Uncertain Identity

The following named taxa are known only on the basis of their fragmentary original descriptions. No specimens are known to be extant for any of these species. Interestingly, most were considered to be bumble bees, or bumble bee ancestors, by their authors. It is likely that none were actually bumble bees or even closely related to the Bombini, but this may never be known with certainty. Three of these names (*Bombus carbonarius, B. pusillus, Bombusoides mengei*) were erroneously listed as *nomina nuda* by Keilbach (1982).

Andrena wrisleyi Salt

Andrena wrisleyi Salt, 1931: 141.

COMMENTS: The description and illustrations of this specimen are adequate to determine that the species was not an *Andrena* or even an andrenid. It is possible that the species was a melittid of some sort that has not subsequently been discovered among newer material. Although the melittid hypothesis is perhaps the best possibility, the original description and particularly Salt's figure of the wing venation are enigmatically suggestive of an electrapine. Although the figure of the hind tibia does not show a corbicula, the description provided of the hind leg by Salt does not match his figure and is somewhat suggestive: ". . . tibiae triangular, much widened apically, . . ." (Salt, 1931: 142). The wing venation is quite similar to species of both *Electrapis* and *Protobombus* (if an electrapine, *Andrena wrisleyi* would fall close to, or in, *Electrapis* owing to the elongate metabasitarsus). It seems hard to imagine but it is possible that Salt's specimen was actually an unknown corbiculate apine in the Electrapini! The holotype was deposited in the ill-fated University of Königsberg and was not subsequently located in any other institution. None of the bees before me can be readily associated with Salt's "*Andrena*" and so I have not designated a neotype. The name must be relegated to incertae sedis.

Bombus carbonarius Menge

Bombus carbonarius Menge, 1856: 27.

COMMENTS: The size and general habitus of *B. carbonarius* from Menge's description suggest a species of *Electrapis*; however, this is entirely conjectural. There is not enough information to confidently assign this species to any of the several "*Bombus*-like" genera.

Bombus muscorum Roussy

Bombus muscorum Roussy, 1937: 58. *Nomen praeoccupatum* (*nec* Linnaeus, 1758).

COMMENTS: The name for this species must eventually be changed as it is a junior secondary homonym of Linnaeus's *Apis muscorum,* which has been considered a valid species of *Bombus* for well over a century. The type was deposited in Roussy's private collection and is now presumably lost. As mentioned above, this species is likely not a true bombine at all; Roussy (1937) himself considered this specimen to be representative of a solitary bee, while all bombines are known to be social, a fact universally known in Roussy's time.

Bombus pusillus Menge

Bombus pusillus Menge, 1856: 27.

COMMENTS: A supposed bumble bee that was described as ". . . ist kaum 3 mill. lang und 1 mill. breit. Behaarung gelblich weisz, auf dem brustrücken zottig." (Transl. ". . . is scarcely three millimeters long and 1 millimeter wide. Pilosity yellowish-white, of the thoracic dorsum shaggy"; translation of the author). It is hard to imagine what this species might have been (perhaps a spheciform or other aculeate?). If indeed a bee, then it was certainly one of the smallest in Baltic amber.

Genus *Bombusoides* Motschulsky

Bombusoides Motschulsky, 1856: 28. Type species: *Bombusoides mengei* Motschulsky, 1856, monobasic.

COMMENTS: Refer to Comments provided for the type species (below).

Bombusoides mengei Motschulsky

Bombusoides mengei Motschulsky, 1856: 28.

COMMENTS: Motschulsky's treatment of this specimen is exceedingly short and provides no clue as to what the bee may have actually been. The entire reference to this bee consists of the clause "... entre autres une très belle *Andraena* [sic] et un *Bombus* nain d'a peine 1 ½ ligne de longueur, que je me permets de dédier à M. Menge, en le nommant *Bombusoides Mengei.*" (Transl. "... among others a very beautiful *Andrena* and a dwarf *Bombus* scarcely 1.5 lines in length, which I allow myself to dedicate to Monsieur Menge, with the name *Bombusoides mengei*"; translation courtesy M. G. Rightmyer). There is no way to associate this name with any of the smaller bees presently known from Baltic amber and thus the name must be relegated to incertae sedis.

CLADISTIC ANALYSES

Cladistic analyses were undertaken in order to both acquire an understanding of the phylogenetic position of particular fossil taxa and to explore the potential effects on hypotheses of relationships previously based solely on Recent species. Data matrices were constructed in WINCLADA (Nixon, 1999) and submitted from there for analysis by NONA (Goloboff, 1993). An initial search was made on each matrix using the *wh** command to identify a single tree or set of trees upon which more exhaustive branch swapping was undertaken using the *max** command. Topologies were visualized and printed using WINCLADA (Nixon, op. cit.).

LITHURGINAE

No previous attempt has been made to cladistically reconstruct lithurgine relationships. Three recent genera have generally been recognized: *Trichothurgus, Microthurge,* and *Lithurgus*; the last has two subgenera, *Lithurgopsis* and *Lithurgus* proper (Michener, 1983). Michener (1983) discussed characters supporting the monophyly of the subfamily and presented an argument for the relationships among these three genera as *Trichothurgus* (*Microthurge* + *Lithurgus*). Herein I have examined representatives of each genus-group taxon inclusive of both subgenera of *Lithurgus* and *Lithurgomma,* a junior synonym of *Trichothurgus* (sensu Michener, 1983, 2000a). Like Michener (1983), I could find no qualitative character to differentiate *Lithurgomma* from *Trichothurgus* and therefore, when coding the matrix, chose to retain these taxa as synonymous. The subgenera of *Lithurgus,* however, could be qualitatively diagnosed, as could the enigmatic Australian species *Lithurgus rubricatus* Smith (1853), and each was coded individually in the matrix. Ten characters of adult external morphology were identified and coded for the recent lithurgines, the fossil genus *Protolithurgus,* and the basal megachilid subfamily Fideliinae (used as an outgroup). The resulting data matrix is presented in table 11, while character definitions are provided in table 10. Analysis of the data matrix resulted in a single topology of length 11, CI 0.88, and RI 0.90 (fig. 116).

TABLE 10
Characters Used in Cladistic Analysis of Lithurginae

0.	Third labial palpus: directed laterally (0); on same axis as second (1).
1.	Female mandible: with two teeth (0); with three teeth (1).
2.	Female lowest mandibular tooth: longer than other teeth (0); shorter than second tooth (1).
3.	Outer surface of tibiae: not spiculate (0); covered by coarse, hairless spicules (1).
4.	Metabasitarsus: flattened (0); cylindrical (1).
5.	Female claw: toothed (0); simple (1).
6.	Female arolia: absent (0); present (1).
7.	Male arolia: absent (0); present (1).
8.	Female T1: convex in profile (0); flattened in profile (1).
9.	Female pygidial plate: not projecting as spine (0); projecting as spine (1).

The relationships proposed by Michener (1983) are generally in accord with those presented here (fig. 116). *Protolithurgus* is placed as sister to all other lithurgines owing to the plesiomorphic retention of a flattened metabasitarsus (typical of other bees), two mandibular teeth, and absence of spicules on the tibiae. Another feature apparently uniting the living genera is the elongation of the proboscis; however, this quantitative character showed little discrete differentiation from

TABLE 11
Data Matrix for Analysis of Generic Relationships of Lithurginae
(Character descriptions presented in table 10)

	0	1	2	3	4	5	6	7	8	9
FIDELIINAE	0	0	0	1	0	0	1	1	0	0
†*Protolithurgus*	?	0	0	1	0	0	1	?	1	?
Trichothurgus	1	1	0	0	1	1	0	1	1	0
Lithurgus s.s.	1	1	1	0	1	1	0	0	1	1
Lithurgopsis	1	1	1	0	1	1	0	1	1	1
Microthurge	1	1	1	0	1	0	0	0	1	1
Lithurgus rubricatus	1	1	1	0	1	1	0	1	1	1

some fideliines and alternative states could not be consistently and unambiguously assigned. For this reason the elongation of the proboscis was not included in the data analysis but the general congruence of this feature with the resulting topology is interesting and noteworthy. Although *Protolithurgus* seems to possess an enigmatic combination of characters unique among megachilids, the genus does share with other Lithurginae the distinctive flattened, first metasomal tergum with a rounded apical margin, a feature found only in lithurgines and which unambiguously unites the fossil with this clade. The genus *Trichothurgus,* as in Michener's system, is sister to all other extant lithurgine genera owing to the lowest mandibular tooth being longer than those above it and the nonprojecting pygidial plate in females. Unexpectedly, the genus *Microthurge,* although itself likely monophyletic, was sister to *Lithurgus* exclusive of *Lithurgopsis* and *L. rubricatus.* The monophyly of *Lithurgus* should be carefully scrutinized as this preliminary analysis could not support the group as it has been traditionally defined. The subgenus *Lithurgopsis* should perhaps be accorded generic rank and *L. rubricatus* transferred to its own genus. It must be noted that the phylogeny presented here is preliminary. A more thorough analysis of lithurgine relationships is needed before major classificatory changes are made to the living genera. I have placed all extant genera in a nominate tribe (with Trichothurgini Moure as a junior synonym), while the fossil is sufficiently distinct to warrant the recognition of a monogeneric tribe sister to Lithurgini (see Protolithurgini, above).

Xylocopinae

Sakagami and Michener (1987) investigated tribal relationships with the Xylocopinae,

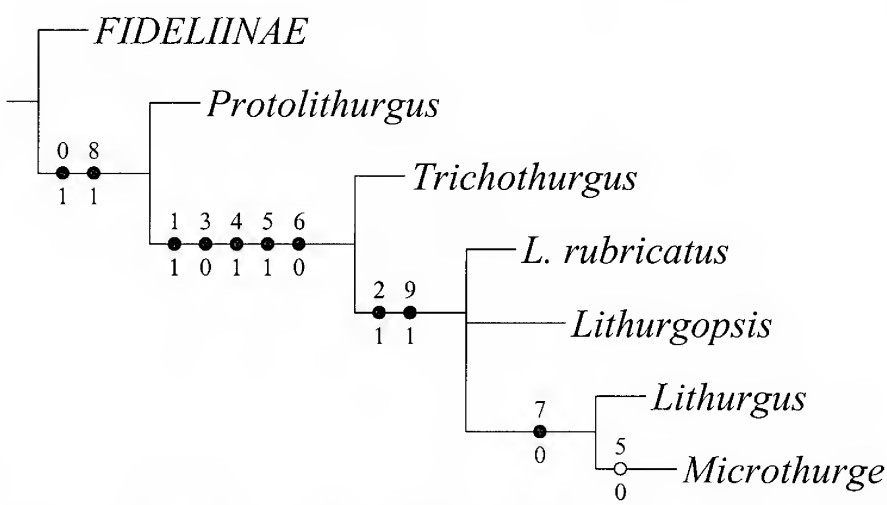


Fig. 116. Phylogeny of Lithurginae based on cladistic anlaysis of data presented in table 11 (Length 11, CI 0.88, RI 0.90). Black dots are unreversed changes; white dots homoplastic character transitions. The character number is indicated above the branch and the state change is indicated below. Fideliinae is the outgroup.

TABLE 12
Characters Used in Cladistic Analysis of Xylocopinae

0.	Lateral margins of clypeus: straight or nearly so (0); concave (1); biconvex (2).
1.	Position of anterior tentorial pit: upper half of clypeus (0); middle of clypeus (1).
2.	Basal elevated area of labrum: absent (0); present (1).
3.	Mandible: tapering from base (0); abruptly narrowed (1).
4.	Alar papillae: absent (0); present (1).
5.	Number of submarginal cells: three (0); two (1).
6.	Prestigma: elongate (0); short (1).
7.	Metabasitibial plate: absent (0); present (1).
8.	Pygidial fimbria: absent or greatly reduced (0); present (1).
9.	Pygidial plate: absent or greatly reduced (0); present (1).
10.	Distal process of metabasitarsus: absent (0); present (1).
11.	Apical metasomal terga: convex (0); flattened (1).
12.	Metatibial scopa: dense (0); reduced (1).
13.	Length of F1: greater than combined lengths of F2–3 (0); shorter than combined lengths of F2–3 (1).
14.	Hind wing first abscissa M: longer than 0.5 times length of second abscissa of M+Cu (0); shorter than 0.5 times length of second abscissa of M+Cu (1).

although they assumed this group to be sister to the corbiculate Apinae (Apidae in their system) and used this group, particularly the basal tribe Euglossini (see below), for a priori character polarizations. They concluded that the monogeneric tribe Manueliini was sister to all other xylocopines and that *Xylocopa* (Xylocopini) was intermediate between *Manuelia* and a Ceratinini + Allodapini clade. As part of a more exhaustive study on long-tongued bee tribal relationships, Roig-Alsina and Michener (1993) demonstrated that the xylocopines were more basal in apid phylogeny and not closely allied to the corbiculates. Furthermore, they concluded that the relative positions of Xylocopini and Manueliini from the earlier study were in fact reversed. Thus, the topology of xylocopine relationships was Xylocopini (Manueliini (Ceratinini + Allodapini)).

TABLE 13
Data Matrix for Analysis of Tribal Relationships of Xylocopinae
(Character descriptions presented in table 12; the one multistate is nonadditive)

	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
Exomalopsis	0 0 1 0 1 0 1 1 1 1 1 0 0 0 0
Xylocopa	0 0 1 0 1 0 0 1 1 1 1 0 1 0 0
Manuelia	0 0 1 0 0 0 1 1 1 1 1 0 1 1 0
Ceratina	1 1 0 1 0 0 1 1 0 0 0 0 1 1 0
†*Boreallodape*	1 1 0 1 0 1 1 0 0 0 0 0 1 1 0
Allodape	2 1 0 1 0 1 1 0 0 0 0 1 1 1 1
Macrogalea	2 1 0 1 0 1 1 0 0 0 0 1 1 1 1

In order to determine the phylogenetic placement of the enigmatic Baltic amber xylocopines (i.e., *Boreallodape*) a character matrix was constructed to explore relationships among the tribes of the subfamily. Fifteen characters were identified and coded for the sole genus of Xylocopini (*Xylocopa* sensu Minckley, 1998), the sole genus of Manueliini (*Manuelia*), one of the two genera of Ceratinini (*Ceratina*), and two genera of Allodapini (*Macrogalea* and *Allodape*). The two genera of allodapines were selected to represent phylogenetic diversity within the tribe based on the cladistic studies of Michener (1977) and Reyes (1998). The genus *Exomalopsis* was used as an outgroup. Characters identified for analysis are presented in table 12, while the complete matrix is presented in table 13. Analysis of the data produces a single topology of length 16, CI 1.00, and RI 1.00. The topology is depicted in figure 117.

The results of this analysis are in complete accord with the analysis of Roig-Alsina and Michener (1993) in that Xylocopini is basal within the subfamily owing to the plesiomorphic retention of alar papillae and an elon-

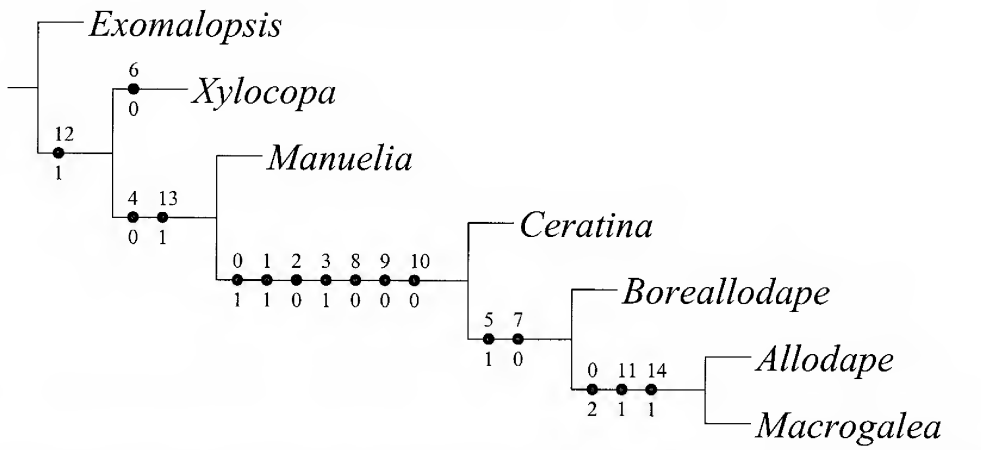


Fig. 117. Phylogeny of Xylocopinae based on cladistic analysis of data presented in table 13 (Length 16, CI 1.00, RI 1.00). Black dots are unreversed changes; white dots homoplastic character transitions. The character number is indicated above the branch and the state change is indicated below. *Exomalopsis* is the outgroup.

gate first flagellomere. The Ceratinini, Allodapini, and *Boreallodape* are grouped together in a well-supported clade (fig. 117). This group is most notable for the abruptly narrowed mandibular structure (e.g., fig. 54). The analysis demonstrates that *Boreallodape* is most closely related to the Allodapini, both groups sharing the presence of two submarginal cells and the absence of the metabasitibial plate. As discussed above (under the description of the tribe Boreallodapini) differences between the Allodapini and *Boreallodape* are significant and inclusion of the latter as the basalmost member of the former would mask the enigmatic features of the fossil among xylocopines. *Boreallodape* is as distinctive as any of the other tribes of the subfamily and recognition of a separate tribe for this group is well supported. It is biogeographically interesting to note that *Boreallodape* is sister to the Allodapini, a group today primarily distributed in sub-Saharan Africa, Asia, and Australia. Among the allodapines only the genus *Exoneuridia* occurs in the West Palearctic and extends as far north as the Mediterranean region in the southeastern half of Turkey (Terzo, 1999). However, a historical biogeographic analysis of the allodapines derived from the recent cladogram of Reyes (1998) suggests that the extant groups of the tribe as a whole are perhaps of a sub-Saharan African origin and that *Exoneuridia* represents a subsequent dispersal into Asia Minor. Most likely, the proto-allodapines (perhaps together with proto-boreallodapines) were of an original Gondwanan origin (as is likely the same for several bee tribes and subfamilies) and the group as we recognize it today diversified in sub-Saharan Africa, subsequently radiating further as they dispersed in the Old World. Under either scenario, *Boreallodape* serves as another example of Baltic amber fossils related to groups now found in Asia or sub-Saharan Africa (see below under Discussion).

Corbiculate Apinae

Relationships among the corbiculate bees have been controversial as have their implications for understanding the evolution of eusocial behavior in this group of bees. As was briefly discussed above, in the modern fauna there are four well-defined tribes: Apini (honey bees), Bombini (bumble bees), Euglossini (orchid bees), and Meliponini (stingless bees). Of these four, the Bombini, Apini, and Meliponini are all eusocial, although advanced eusociality (i.e., those societies with morphologically differentiated queen and worker castes) is found only in Apini and Meliponini (not just among cor-

biculates, but among all of the Apoidea). Of the 15 possible rooted topologies for four taxa, eight have been proposed at one time or another for the living corbiculates based on either a priori interpretations of the same 10–20 morphological characters, single character analyses, or studies of limited DNA sequences. Outgroup-based cladistic analysis of morphological evidence produced a single, fully resolved topology (Prentice, 1991; Roig-Alsina and Michener, 1993; Chavarría and Carpenter, 1994; Schultz et al., 1999). This topology supports the "single origins" hypothesis whereby both general eusocial behavior and advanced eusocial behavior arose once in a hierarchical fashion. Thus, eusociality arose in the common ancestor of the Bombini, Meliponini, and Apini, while advanced eusociality arose in the common ancestor of Meliponini and Apini. Molecular analyses have produced alternative cladograms that are not consistent with this scenario, nor are they always consistent with themselves (e.g., Cameron, 1991, 1993). These analyses imply either dual origins of advanced eusocial behavior or ambiguous reconstructions by uniting the bumble bees and stingless bees. A simultaneous analysis of these DNA sequences with morphological data produces topologies that support the single origin for advanced eusocial behavior by reuniting the Meliponini and Apini (Chavarría and Carpenter, 1994; Schultz et al., 1999). However, while these combined studies typically also support a single origin for general eusociality, the support is not as strong. Thus, a clear resolution has yet to be achieved concerning relationships among these tribes and the addition of more characters and more taxa to analyses is needed. Since most characters used in morphological studies of the tribes are fixed across taxa within each tribe, added taxa of living representatives provide little information for resolution of relationships outside of more accurately reconstructing the basal node of each respective tribe. Most of the Baltic amber corbiculates as demonstrated above, however, do not fall into the living tribes and possess combinations of characters unknown in any of the living lineages. Thus, the addition of these groups to analyses may have important implications for understanding corbiculate relationships. Herein I have both expanded the available morphological data as well as the taxon representation (tables 14, 15). The character-state matrix is presented in table 15. Analysis of these data produces two most parsimonious topologies (length 65, CI 0.81, RI 0.93), the strict consensus of which is depicted in figure 118. Of the two trees, only one of the resultant topologies is strictly supported (Nixon and Carpenter, 1996) and is identical to the consensus (fig. 118). The analysis produces a nested set of relationships, with numerous groups breaking up some of the long branches between the living tribes. More importantly, these results produce a hierarchy of intermediary lineages separating the advanced eusocial tribes (i.e., Apini and Meliponini) from the bumble bees and orchid bees. Topologies attempting to unite Bombini with Meliponini cannot remotely account for the character combinations exhibited by the fossil taxa. That this hierarchy is congruent with behavioral characters and other biological traits (e.g., Noll, 1998) is noteworthy. Thus, quite contrary to the view asserted by Patterson (1981), paleontological data has had a significant impact on our understanding of corbiculate bee relationships. Interestingly, the corbiculate bees are a nice example of the type of group wherein fossils are hypothesized to be most important for phylogeny reconstruction. Gauthier et al. (1989: 193) hypothesized, "... fossils should be most important in phylogenetic inference when the group of interest is old and only a few, highly modified, terminal taxa are extant". The extant tribes of corbiculate bees are highly derived with numerous synapomorphies supporting each, and the tribes are undoubtedly ancient—extending into the Late Cretaceous, as shown by the presence of a true meliponine in amber of probable Maastrichtian age (Michener and Grimaldi, 1998a; Engel, 2000b; see also below under Origin of Bees). Under such conditions intermediary fossil lineages are critical for evaluating relationships among the surviving lineages.

The reconstruction of social behavior on the cladogram may, at first glance, appear to be problematic owing to the absence of direct observations for the social state of the fossil taxa. It is possible, however, to infer behav-

TABLE 14
Characters Used in Cladistic Analysis of Corbiculate Apinae
(Characters 35 and 48 additive; all others nonadditive)

0.	Paraocular carina: absent (0); present (1).
1.	Anterior condyle: contiguous with clypeal border (0); partly covered by clypeal border (1).
2.	Lateral expansion internal thickenening above epistomal sulcus: at least as wide as one-half antennal socket diameter (0); reduced, i.e., less than one-half antennal socket diameter (1).
3.	Postoccipital pouch below foramen magnum: absent (0); present (1).
4.	Stipital concavity: absent (0); present (1).
5.	Galeal blade: uniformly sclerotized except at apex (0); posterior margin broadly unsclerotized (1).
6.	Stipital sclerite: distinct (0); fused to stipes (1).
7.	Submentum and mentum: fused (0); distinct (1).
8.	Submental spine: absent (0); present (1).
9.	Glossal rod: not enclosing bacular canal (0); surrounding bacular canal (1).
10.	Female mandible: slender (0); pollex expanded (1).
11.	Outer mandibular grooves: distinct (0); largely absent (1).
12.	Lateral carina separating exposed part of propleuron: present (0); absent (1).
13.	Apophyseal pit of prosternum: present (0); absent (1).
14.	Prosternal shape: not or weakly constricted (0); strongly constricted (1).
15.	Metatibial spurs: two present (0); one present (1); absent (2).
16.	Metabasitibial plate: present at least in female (0); absent (1).
17.	Rastellum: absent (0); present (1).
18.	Auricle: absent (0); present (1).
19.	Corbicula: absent (0); present (1).
20.	Strigil: without anterior velum (0); with anterior velum or thickening (1).
21.	Arolia: present (0); absent (1).
22.	Submarginal cells: three (0); none (1).
23.	Wing pubescence: setose throughout (0); partly bare (1).
24.	Alar papillae: absent (0); present (1).
25.	Marginal cell apex: closed (0); open (1).
26.	Jugal lobe of hind wing: present (0); absent (1).
27.	Jugal comb: absent (0); present (1).
28.	Female T5 prepygidial fimbria: present (0); absent (1).
29.	Female T6 pygidial plate: present (0); absent (1).
30.	Male T7 apex: entire (0); developed into two conical points (1).
31.	Male gonostylus: articulated to gonocoxite (0); indistinctly fused (1).
32.	Volsella: free sclerite (0); absent or fused (1).
33.	Male metatibia: unmodified (0); modified (1).
34.	Compound eye setae: minute or absent (0); elongate (1).
35.	Gonobase: absent (0); present and reduced (1); present and normal (1).
36.	Forewing 1m-cu: long and oblique (0); short and angled (1).
37.	Prosternal setae: present (0); absent (1).
38.	Basisternum: normally developed (0); enlarged (1).
39.	Metapleural ridge: extending to posterolateral corner of mesopleuron (0); not meeting posterolateral corner of mesopleuron (1).
40.	Basistipital process: normal (0); present (1).
41.	Sting: absent or vestigial (0); present (1).
42.	Penicillum: absent (0); present (1).
43.	Sternal groove: absent (0); present (1).
44.	Claws: cleft (0); simple (1).
45.	Basal vein: near cu-a (0); strongly distad cu-a (1).
46.	Forewing 1rs-m: short, orthogonal to M (0); elongate, oblique to M (1).
47.	Distal hamuli: numerous, 11 or more (0); reduced, 8 or fewer (1).
48.	Sociality: solitary or communal (0); primitively eusocial (1); advanced eusocial (2).
49.	Supraalar carina: absent (0); present (1).
50.	Pterostigma: reduced, small (0); large (1).

TABLE 15
Data Matrix for Analysis of Tribal Relationships Within the Corbiculate Apinae
(Character descriptions presented in table 14)

	1111111111222222222233333333334444444444 5
	0123456789012345678901234567890123456789012345678901234567890
Anthophora	0101100010000000000000001100000101002000001000000010
Centris	0100100010000000000000101100000101002000001000000010
Xylocopa	0100101100000000000000101100010011002000001000000010
Apis (Apis)	0010100101111111211111000000011011010111111000110210
Apis (Megapis)	0010100101111111211111000000011011010111111000110210
Apis (Micrapis)	0010100101111111211111000000011011011111111000110210
Melipona	0010000101111112110100100100110010011111100101??201
Liotrigona	0010000101111112110100100100110010011111100101?1201
Bombus	0000100100101000111111001010110000002001101000000110
Euglossa	1101110010101000111111001011110001020000010100000010
Eufriesea	1101110010101000111111001011110001020000010100000010
Eulaema	1101110010101000111111001011110001020000010000000010
†*Kelneriapis*	00????0????11???211010010010011????0?1????01010?1?01
†*Liotrigonopsis*	00????0????11???211010010010011????0?1????01010?1?01
†*Melikertes*	00??10????11???111110000000011????0?1????1000001?11
†*Succinapis*	00??10????11???111110000000011????0?1????1000001?11
†*Melissites*	00??10????11???111110000000011????0?1????1000001?11
†*Roussyana*	00??10????11???111110000000011????0?1????1000001?11
†*Electrapis*	00??10????10?001111110000000011????0?0????1000000?11
†*Protobombus*	00??10????10???111111000000011????0?0????1000000?11
†*Thaumastobombus*	00??10????10???111111000000011????0?0????1000001?11
†*Electrobombus*	00??10????10???011111000100011????0?0????1000000?10

ioral character information from fossils either through **1.** particular morphologies that are tightly correlated or unique to a given ethological trait (e.g., Michener and Grimaldi, 1988b; Poinar, 1991; Engel, 1998c, 2000b; Simmons and Geisler, 1998); **2.** "concrete behaviors" (e.g., nest architecture, footprints), whereby the products of a behavioral repertoire are preserved as trace fossils either in association with the remains of the organism or in isolation (e.g., Carpenter, 1992; Genise and Hazeldine, 1998; Lockley and Matsukawa, 1999); **3.** preservation of the individual while in the act of performing some portion of a particular behavioral repertoire (e.g., Norell et al., 1995; Clark et al., 1999); or, **4.** phylogenetic inference (e.g., Michener and Grimaldi, 1988b; Engel, 1998c, 2000b). As mentioned above, advanced eusocial societies are recognized by morphologically differentiated queen and worker castes, and this attribute is known only for these societies. Among the fossils, all except the single individual of *Electrobombus* exhibit the reduced metasomal structure (and to a lesser degree a barbed sting) typical of workers; indicating that they were members of advanced eusocial societies (fig. 119). Thus, although the fossils were coded and analyzed as unknown for their social state, all except *Electrobombus* could essentially have been coded as "advanced eusocial". The fact that those taxa with worker-caste morphologies cladistically group with the Apini and Meliponini (fig. 119) reinforces the reconstruction of a single origin for advanced eusocial behavior in the bees. Moreover, the position of *Electrobombus* within a clade of already eusocial (either primitive or advanced eusocial) lineages implies, via phylogenetic inference, eusocial behavior to some degree in this taxon (fig. 119). In summary, taking all of this information into account produces a single possible reconstruction of eusocial evolution within the corbiculate bees. The available evidence supports only the "single origins" scenario wherein general eusociality arose once in the common ancestor of the Bom-

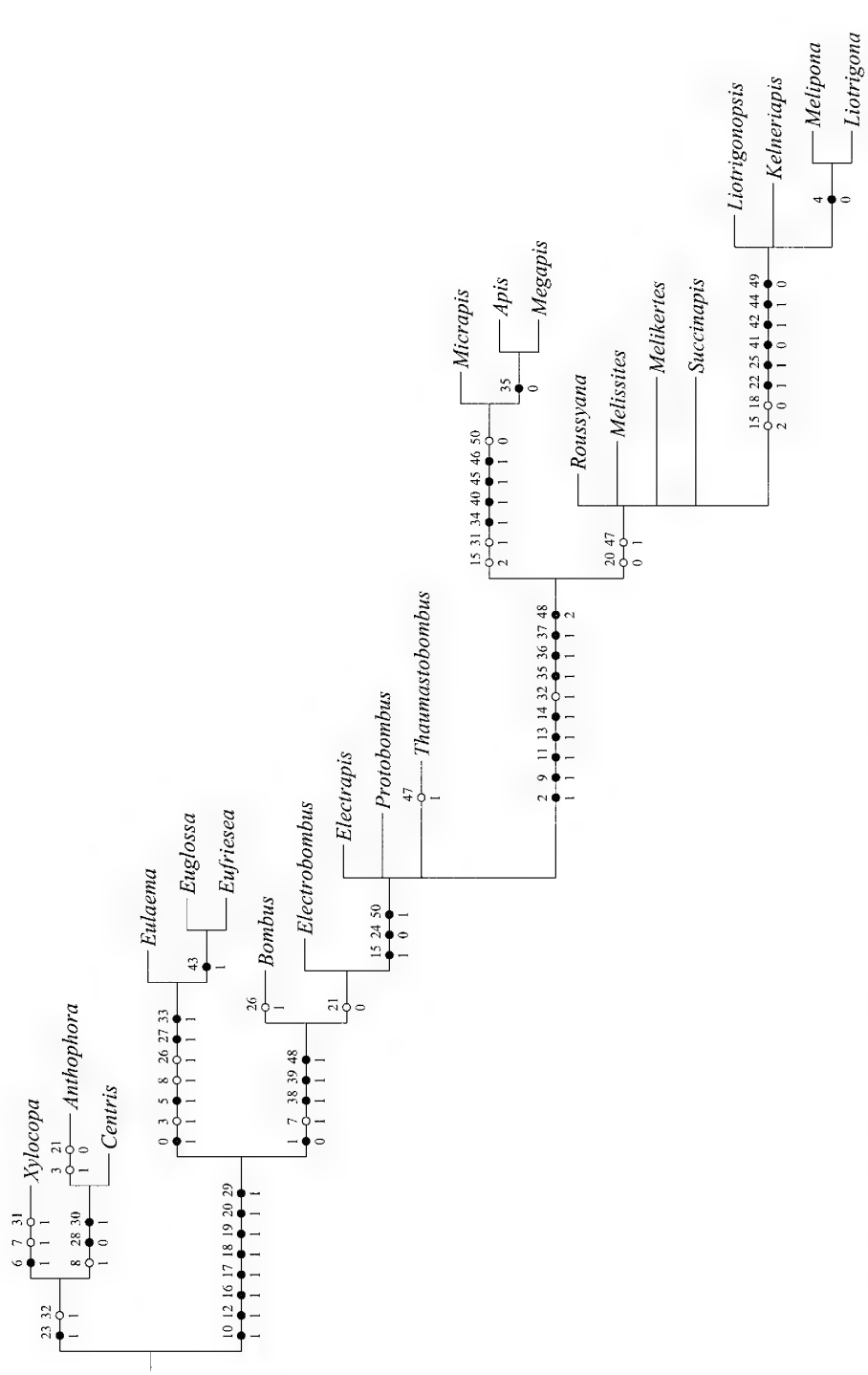


Fig. 118. Phylogeny of corbiculate Apinae based on cladistic analysis of data presented in table 15 (Length 65, CI 0.81, RI 0.93). Black dots are unreversed changes; white dots homoplastic character transitions. The character number is indicated above the branch and the state change is indicated below. *Anthophora, Centris,* and *Xylocopa* are the outgroups.

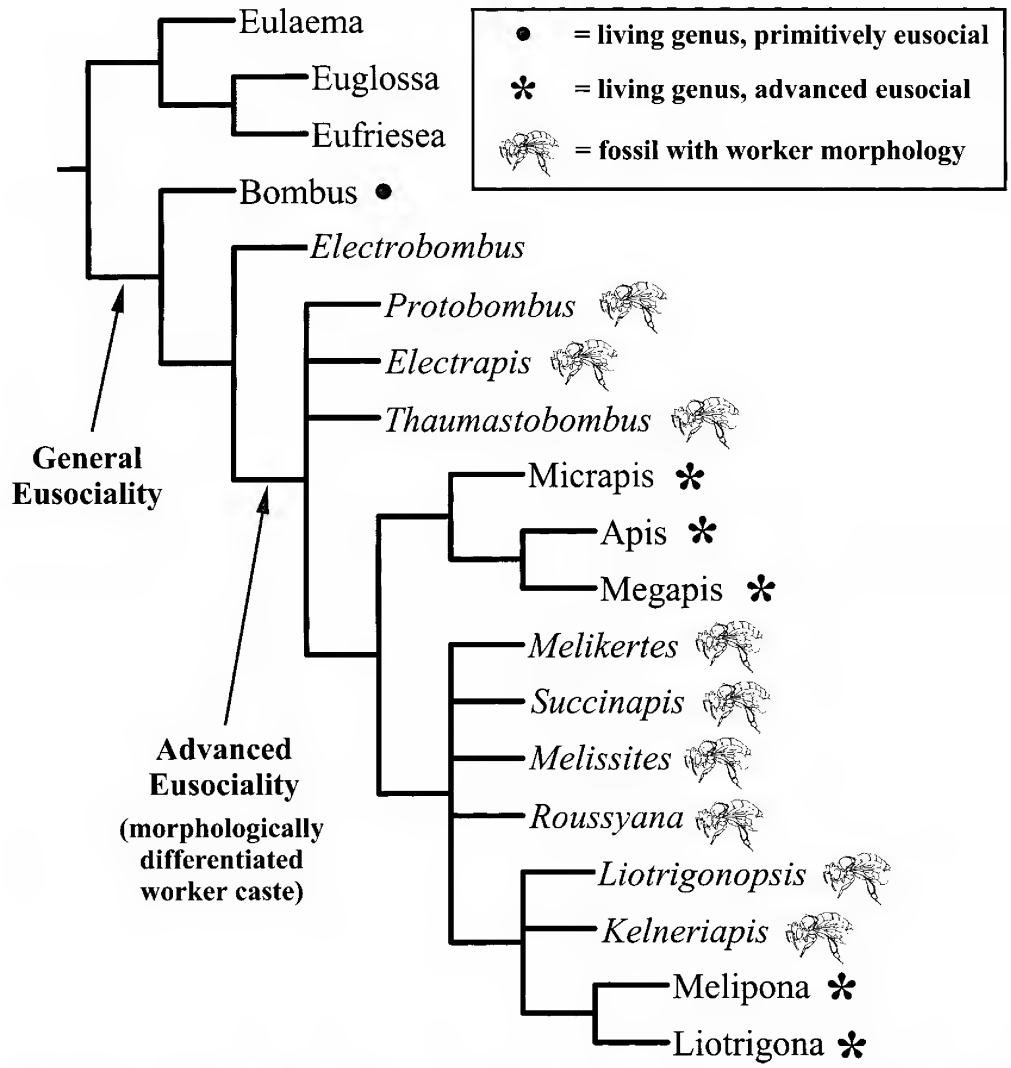


Fig. 119. Distribution of social ethotypes among the corbiculate apines as well as fossils exhibiting worker morphologies. The euglossine genera (*Euglossa, Eufriesea,* and *Eulaema*) are generally communal or solitary, while the outgroups (not depicted here) are solitary. Extinct genera are italicized.

bini, Electrobombini, Electrapini, Melikertini, Apini, and Meliponini with a subsequent, single evolutionary elaboration of this trait to advanced eusociality in the common ancestor of at least the Electrapini, Melikertini, Apini, and Meliponini (fig. 119) (Engel, in press-b).

Recently, new studies of DNA sequences have attempted to provide further support for a Meliponini + Bombini clade (Koulianos et al., 1999; Mardulyn and Cameron, 1999). Interestingly, a simultaneous analysis of morphological characters and of the sequence data published by Koulianos et al. (1999) produces a "single origins" topology. These sequence data are particularly problematic in that they employ mitochondrial DNA regions (like the earlier studies of Cameron, 1991, 1993) commonly used in species-level anal-

yses owing to high levels of interspecific variation. For example, analysis of the earlier mitochondrial DNA data for relationships among species within a given genus were more internally congruent than when examining older relationships (Engel and Schultz, 1997; Schultz et al., 1999). That the corbiculate tribes are undoubtedly ancient only serves to reinforce the need for careful selection of gene regions when undertaking an analysis, particularly in a group that extends back into the Mesozoic [the divergence among the tribes being at least 75 Ma owing to the presence of a true meliponine in Late Cretaceous amber (Engel, 2000b)]. The data of Mardulyn and Cameron (1999) are an improvement over those of previous studies by attempting to select relatively conserved gene regions, but Ascher and Danforth (in rev.) have demonstrated that there are numerous other critical problems with these sequence data and analyses. Moreover, all of these studies have suffered from poor taxon sampling and choice of outgroups. Thus, the available sequence data are not at all reliable and a well approached (e.g., choice of ingroup taxa, choice of outgroup taxa, number of taxa examined, number of informative characters, choice of gene region) molecular analysis remains to be undertaken for the corbiculate Apinae.

Perhaps one of the more interesting morphological implications of the fossil corbiculate taxa and the cladistic analysis presented here concerns the evolution of the metatibial spurs. The apomorphic absence of metatibial spurs in the Apini and Meliponini has often been used as one of several traits uniting these two tribes in analyses of the living taxa; the presence of two metatibial spurs is plesiomorphically found in the outgroups, euglossines, and bombines. Those Baltic amber corbiculate genera that do not cladistically fall into any of the extant tribes have a single, often reduced, metatibial spur (difficult to see in many specimens). The taxa exhibiting this "one spur" character-state form a paraphyletic assemblage derived from a two-spurred ancestor and subsequently giving rise to the Apini and Meliponini, neither of which have metatibial spurs. This pattern itself is intuitively pleasing in that it implies a gradual reduction in the number of metatibial spurs. Surprisingly, however, the Apini and Meliponini are separated by a group of extinct taxa that are sister to the Meliponini (i.e., the Melikertini) and that have a single metatibial spur. Thus, the implication is that the loss of spurs in the honey bees and stingless bees is not a feature shared through common ancestry (i.e., not a synapomorphy for the two tribes); nonetheless, support for their close relationship was not degraded by the loss of this supposed synapomorphy. The apines and meliponines independently lost tibial spurs from a single-spurred ancestor. From the viewpoint of "reciprocal illumination" this interpretation of independent loss makes sense. A reëxamination of the metatibia-metabasitarsus junction in living stingless bees and honey bees reveals two, somewhat different morphologies, suggesting at an observational level the possibility that the homology of absence is incorrect in this case. The inner apex of the metatibia and the junction with the metabasitarsus in honey bees is essentially unmodified; the only significant difference by comparison to "spurred" corbiculate bees is the simple absence of the metatibial spurs. On the other hand, in stingless bees the entire junction between these two leg segments is grossly transmogrified, perhaps partly through the loss of the auricle. In most stingless bee taxa the inner apical region of the metatibia where the metatibial spurs would articulate is modified with a slight impression leading down to the articulation with the metabasitarsus, which itself is highly modified by the complete absence of an auricle. Likewise, the inner apical margin of the metatibia extending posteriorly from this impression where the metatibial spurs would otherwise articulate is weakened; in some instances this is further manifested through a weakening of the rastellum. These two different morphologies of "absence" suggest from examination of living taxa alone that the conditions seen in honey bees and stingless bees are perhaps not homologous and, in fact, represent two separate character states. A paleontological perspective has thus provided illumination toward understanding not only cladistic relationships among the living taxa but also for interpreting their morphol-

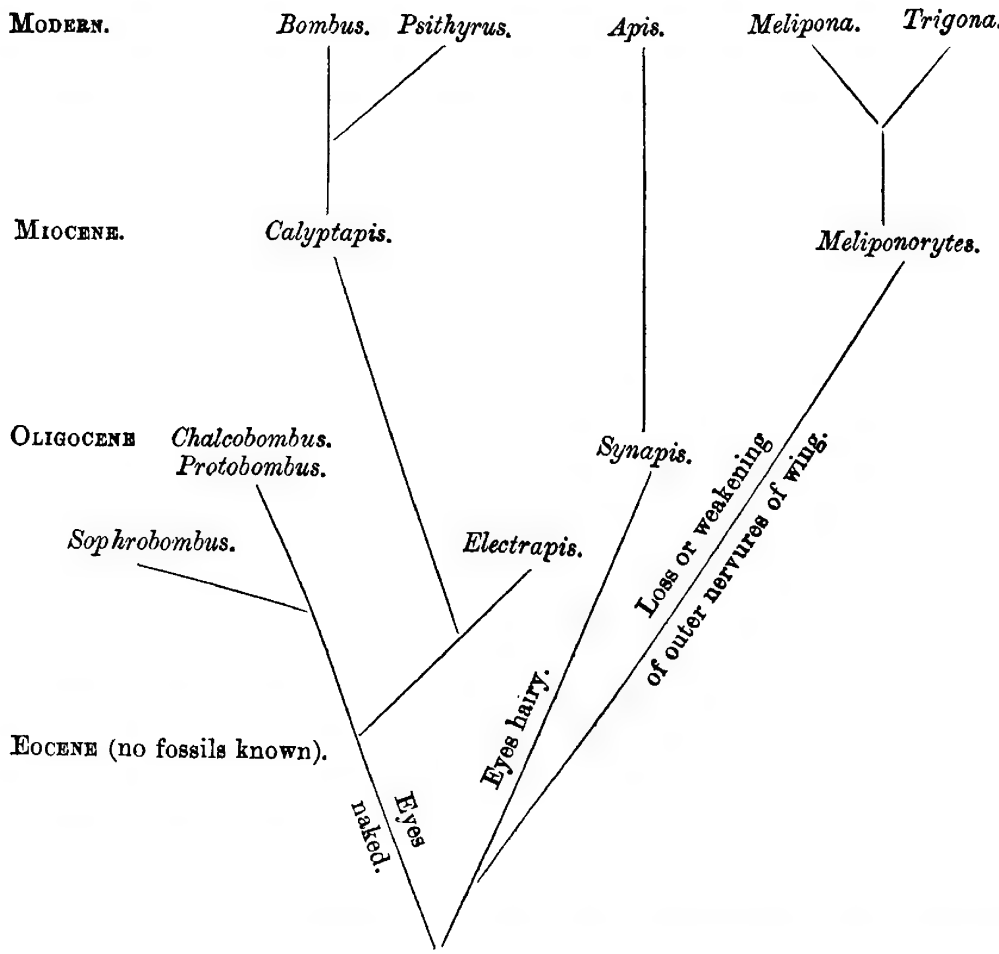


Fig. 120. Hypothesis of relationship for the corbiculate bees as envisioned by Cockerell (reproduced from Cockerell, 1908b). He did not include tribe Euglossini and the ages he used for particular deposits are now understood to be as follows: *Calyptapis* [considered as a junior subjective synonym of *Bombus* by Zeuner and Manning (1976)] is from early Oligocene deposits of Florissant, while the genera *Sophrobombus, Chalcobombus, Protobombus,* and *Electrapis,* all in Baltic amber, are middle Eocene in age. Most species of *Synapis* (a subgenus of *Apis*) are from Oligocene strata but at least two species are from early Miocene deposits (Engel, 1999c, unpubl. data). *Meliponorytes* (described by Tosi, 1896) is either a true fossil in Miocene amber from Sicily or perhaps misidentified in African copal and congeneric with living meliponines (see appendix 1).

ogy via a character-state known only from the fossil record.

The analysis presented here is the first cladistic analysis combining fossil corbiculate genera with living genera. It is, however, not the first phylogenetic attempt to unite the fossil record of corbiculate apines with their extinct counterparts. Cockerell (1908b) presented a phylogeny for this group of bees (excluding the Euglossini) derived from a few characters and a great deal of intuition. His interpretation (fig. 120) is not too different from the one presented here; i.e., Cockerell united the Apini and Meliponini as sister taxa. My interpretation of the fossils differs from that of Cockerell in that he also

used plesiomorphic traits to unite genera; for instance, he brought together those *Bombus*-like groups (e.g., *Electrapis, Protobombus*) on the primitive absence of elongate setae on the compound eyes (fig. 120). A cladistic interpretation of these same taxa based on outgroup comparison (both with the Euglossini as well as non-corbiculate apine tribes) demonstrates that although fossils such as *Electrapis* and *Protobombus* are plesiomorphically similar to bumble bees, these genera share apomorphic traits that unite them more closely to honey bees and stingless bees (fig. 120). Thus, the *Bombus*-like genera form a paraphyletic grade leading to the Apini, Meliponini, and Melikertini (species of the latter were not known to Cockerell, as he had not seen the only described melikertine in his era; i.e., *M. proavus*). Cockerell also considered some of the fossils to be directly ancestral to modern lineages (e.g., the single species of *Synapis* was the ancestor of living *Apis* species). While many of these taxa are indeed plesiomorphic in most respects by comparison to living relatives, none can be interpreted as ancestors of extant lineages. Paraphyletic stem groups that are probably ancestral to large extant families are known in the amber fossil record, a good example being *Prioriphora* (Phoridae), known only in Cretaceous amber (Grimaldi and Cumming, 1999).

DISCUSSION

Origin of Bees

The bees are a derived, monophyletic group of the spheciform wasps (Müller, 1872; Michener, 1944, 2000a; Brothers, 1975, 1999; Lomholdt, 1982; Alexander, 1992; Brothers and Carpenter, 1993; Alexander and Michener, 1995; Melo, 1999), perhaps most closely related to the family Crabronidae (Alexander, 1992; Melo, 1999). Although alternative arguments have been presented that suggest bees to be related to mutillids and formicids (e.g., Börner, 1919; Lanham, 1979, 1980), these hypotheses were based primarily on two characters taken in isolation and have not been supported by any rigorous analysis of aculeate relationships.

Reports of bees from pre-Cretaceous deposits and arising prior to the origin of angiosperms have generated a great deal of controversy (and rightly so) but are, unfortunately, entirely unfounded. The accounts by Hong (1984) and Hong and Miao (1992) of a bee from the earliest Cretaceous of China can be immediately dismissed since this fossil is easily identifiable as a sphecid wasp (Darling and Sharkey, 1990; Michener, 1997; Engel, 1998c, 1999c, 2000b) and in fact has been recently synonymized with the genus *Archisphex* (Rasnitsyn et al., 1998). Similarly, the fossil identified as a "native bee" by Carroll (1962) from the Jurassic of Australia is not actually a bee. Carroll's specimen is a very poorly preserved compression fossil lacking wings and a complete head (see her fig. 1) and cannot therefore be assigned to any insect group with great certainty. It must be noted that no single character is preserved that could place this fossil among the Apoidea (nor even among the Aculeata!).

The reports by Hasiotis and Demko (1996), Hasiotis (1997), Hasiotis et al. (1995, 1998), and Kay et al. (1999) are not based on body fossils but instead on trace fossils from the Jurassic and Triassic of North America. These accounts are fraught with errors, with statements like, ". . . Jurassic bees, like their modern homologs, may have also used carrion for food and nutrients. . . " (Hasiotis and Demko, 1996: 366) and "Triassic hymenopterans may also have scavenged carrion. . . as do some modern species of halictid, anthophorid, trigoniid [sic], and meliponine bees"[7] (Hasiotis et al., 1998: 116) Per common knowledge, bees are exceptional for their use of pollen; they collect and provision their young with a mixture of pollen, nectar, and/or plant oils. Even cleptoparasitic bees feed on pollen, although the mother does not collect the pollen herself. Of the nearly 20,000 described species of living bees, only three species of the highly derived

[7] A small taxonomic note: Enigmatically, Hasiotis et al. (1998: 116) have removed the necrophagous *Trigona* species from the tribe Meliponini and accorded this meliponine genus familial rank as "trigoniids". *Trigona* is a genus of Meliponini; there is no such thing as a "trigoniid". An additional taxonomic problem arises in that Hasiotis and Demko (1996: 366) refer to their nest as the product of ". . . sweat bees in the Anthophoridae and Halictidae". Sweat bees are species of the subfamily Halictinae; other halictids (i.e., rophitines, nomiines) and anthophorines are not sweat bees.

tribe Meliponini are obligate necrophages (Camargo and Roubik, 1991). Despite the claim by Hasiotis et al. (1998), no halictid or anthophorine provisions its nests with carrion. The three *Trigona* necrophages certainly do not represent the groundplan feeding behavior for bees, as they are from a derived genus, of a derived tribe, of the most derived subfamily, of the most derived family of bees. Even if one wanted to argue that the fossil nests represented an extinct species of this derived clade, the position would still be unfounded, as all three construct resinous nests and combs in tree or ground hollows and not branching burrows/galleries in the soil or in wood (Roubik, 1983; Camargo and Roubik, 1991). The large number of cells in the fossil nest described by Hasiotis and Demko (1996) was taken as evidence for eusocial behavior. As has been repeatedly demonstrated for ground-nesting bees (e.g., Sakagami and Michener, 1962; Eickwort and Sakagami, 1979; Engel, 1998b), there is no correlation between nest architecture and level of sociality. Solitary and communal species can make nests just as large and elaborate as semisocial and eusocial species. Hasiotis and Demko's fossil nest shows no single character indicative of bee activity. The presence of flask-shaped cells, the slightly constricted opening, and shafts/corridors are generalized features common to many ground-nesting Hymenoptera, as well as some insects in other orders, so such characters are *not* diagnostic for bees as erroneously suggested by Hasiotis and Demko (1996). The presence of a spiral cell closure is one of the few features suggestive of bee activity (although it also occurs in some other insects) and such a structure was not found with their trace fossils. Otherwise, bee nests in the ground are similar in general plan to many groups of Hymenoptera. Researchers should be far more hesitant to attribute such trace fossils to bees. These same difficulties apply equally to the Triassic trace fossil discovered in a petrified tree in Arizona and popularized by Hasiotis (1997; see also Wilford, 1995), Hasiotis et al. (1995, 1998), and Kay et al. (1999). None of these nests are the products of bees; not only do they lack any characters suggestive of bees, they actually show evidence of having been beetle galleries (see also critique by Grimaldi, 1999, who arrived at the same conclusion). Several modern beetle groups make galleries that are similar to the traces they have recovered. The chemical characteristics presented by Kay et al. (1999) to be diagnostic for primitive bees are in fact not diagnostic for bees at all. Phenetic comparisons in chemical composition are meaningless for a positive identification; what is needed would be an apomorphic chemical trait unique (i.e., fixed and diagnostic) to bees. No such chemical or blend has been identified to date.

Some bee species have been observed to collect pollen from gymnosperms—*Trigona carbonaria* Smith on *Cycas media* Brown (Cycadaceae) (Ornduff, 1991) and *Colletes* sp. on *Juniperus virginiana* Linnaeus (Cupressaceae) (Burnham, 1978)—and this might be seen to lend credence to a pre-angiosperm origin for the bees. Such forgaing behavior led both Burnham (1978) and Ornduff (1991) to speculate that bees might be older than flowering plants; however, to truly support such a conclusion one must demonstrate that the groundplan foraging behavior for the bees was on gymnosperm pollen with a subsequent "host-shift" to angiosperms. The foraging activity of the polylectic *T. carbonaria* does not reflect any groundplan foraging behavior for the bees owing to its apomorphic position in the Meliponini (fig. 123). The behavior of the unidentified *Colletes* species is more tantalizing owing to the basal position of this subfamily (albeit not necessarily this genus). However, this foraging behavior is not distributed across a series of basal species in *Colletes,* the Colletinae, or even the Colletidae (or other bee families, for that matter, as would be required for a cladistic reconstruction of gymnosperm foraging in the bee groundplan). *Colletes,* in fact, shares credible larval synapomorphies with the Hylaeinae, Xeromelissinae, and Euryglossinae while the remainder of the Colletinae as it is currently conceived (i.e., the Paracolletini) is more basal (McGinley, 1981). Thus, such an observation in a single species of *Colletes* does not reflect a groundplan trait for the bees. Instead, the foraging activities of a variety of genera across the Paracolletini (as well as numerous other colletid groups) and basal genera of other basic

short-tongued bee families would need to be observed before any such conclusion could be drawn. Until an identifiable *body* fossil of a bee is discovered from pre-Cretaceous sediments (or in association with nest remains), there exists no evidence that bees arose prior to the origin and early diversification of the angiosperms.

A particular problem with claims for a Jurassic or Triassic origin is that they hypothesize, in the absence of any bee fossil, that bees arose prior to Aculeata (in the case of the Jurassic) and before the Apocrita (in the case of the Triassic)! The entire order Hymenoptera does not appear in the fossil record until the Triassic and then only on the basis of the basalmost symphytan family Xyelidae. No apocritan lineage has been found prior to the Jurassic. Bees simply could not have been present in the Triassic since no apocritans or even advanced wood wasps had yet originated. Likewise, in Jurassic deposits the known hymenopterans are basal apocritan lineages, a diversity of symphytans, and a single plesiomorphic family of aculeates. The earliest aculeate fossils are of the extinct family Bethylonymidae from the Uppermost Jurassic of Kazakhstan (Rasnitsyn, 1975) considered to be the sister group to all other aculeates (Rasnitsyn, 1988; Ronquist et al., 1999). All other aculeates in the fossil record have their first appearance in the Cretaceous. Moreover, the earliest members of the Apoidea are plesiomorphic spheciform wasps in Lower Cretaceous sediments of Brazil, Europe, and Central Asia. No single specimen has been found of a more advanced spheciform lineage (e.g., Crabronidae) prior to the Early Cretaceous. As mentioned above, bees are a derived, monophyletic group arising from the paraphyletic assemblage of spheciform families in the Apoidea. Bees, therefore, must have originated *after* the earliest spheciforms. Since spheciforms (and thereby the entire superfamily Apoidea) did not appear until the Cretaceous, bees *must* have originated in the Cretaceous. If one prefers to argue for the oldest possible age of bees, then the uppermost boundary for their age is the earliest part of the mid-Cretaceous, or about 125 Ma. This automatically places the origin of bees after the origin of angiosperms, which themselves either originated in the earliest Cretaceous (Crane et al., 1995) or the uppermost Jurassic (Sun et al., 1998). Thus, the available evidence suggests quite the opposite scenario from those of the aforementioned authors. Bees arose sometime *after* the origin of flowering plants—a long-standing conclusion arrived at by numerous authors (e.g., Michener, 1979; Engel, 1996, 2000b; Grimaldi, 1999) and the only one with available evidence.

Interestingly, the radiation of bees coincides nicely with the period in which angiosperm diversity increased dramatically. The oldest fossil bee presently recorded is *Cretotrigona* in Late Cretaceous (Maastrichtian) amber from New Jersey[8] (Engel, 2000b). *Cretotrigona* is a derived apine of the tribe Meliponini (Apidae: Apinae). Thus, the cladogenetic events that produced all of the lineages between the origin of bees and the branch that eventually gave rise to the meliponines must have taken place prior to the Late Cretaceous. If a cladogram of bee families is overlayed on the geological column and the oldest possible age for bees assumed (fig. 121), then the diversification of bees into higher lineages must have coincided with the angiosperm radiations that took place from 130–90 Ma (Crane et al., 1995), with a particularly dramatic increase in generic diversity 115–90 Ma (Lidgard and Crane, 1988; Crane and Lidgard, 1990). Even if the bees are somewhat younger than the 125 Ma date hypothesized here, they still must have radiated prior to the Late Cretaceous [simply owing to the presence of *Cretotrigona* and the existence of plants today tightly associated with Apinae in 90 Ma deposits (Crepet and Nixon, 1998)]. Thus, the window for both the origin and early diversification of bees into higher lineages lies between ca. 125 Ma and 100 Ma. This period of diversification for bees accords nicely with similar periods in the evolution of derived floral characters associated with insect pollination (Crepet, 1996). There is, at pre-

[8] The Cretaceous age of this amber was questioned by Rasnitsyn (*In* Rasnitsyn and Michener, 1991) and considered to be Paleocene. Grimaldi (1999), however, has argued convincingly for a Cretaceous age of this deposit and the Late Maastrichtian age (65–70 Ma) is adopted here [see also Engel (2000b)].

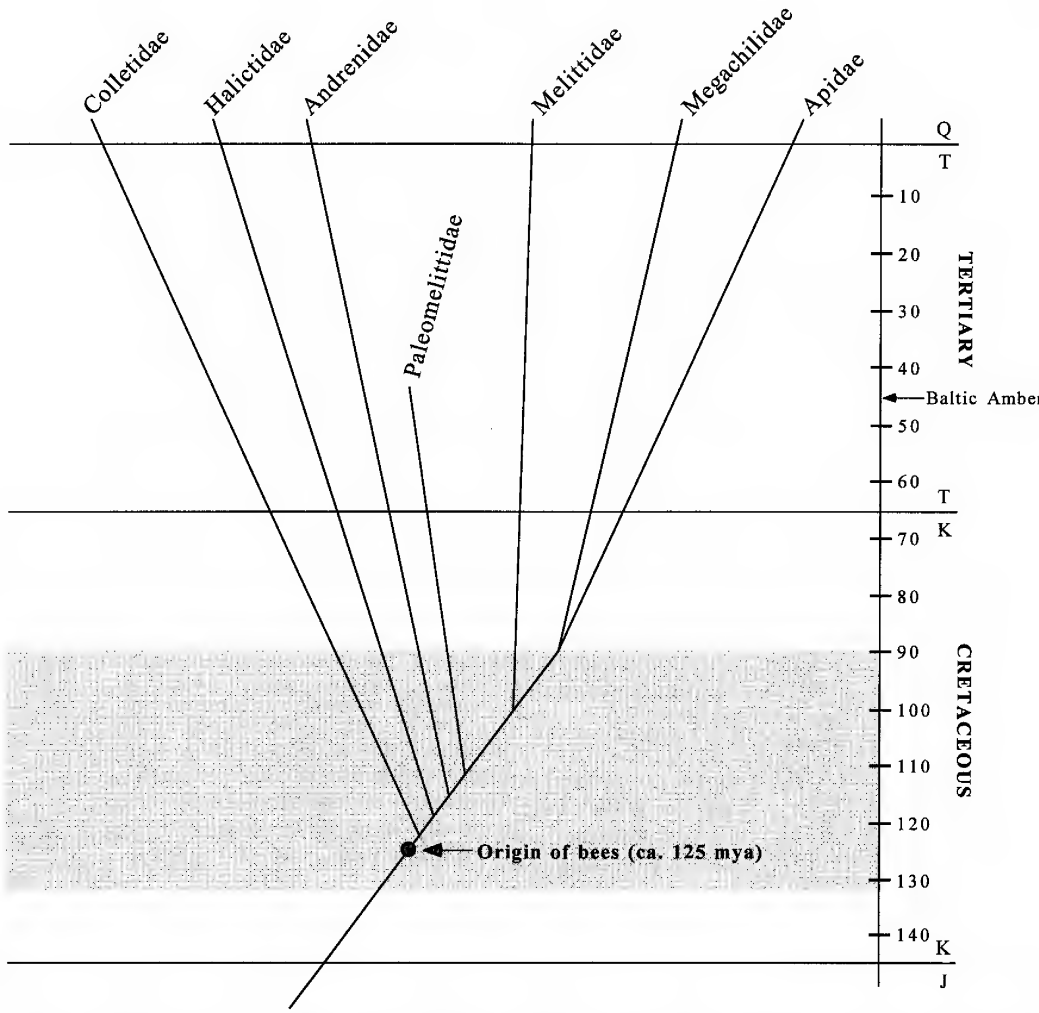


Fig. 121. Phylogeny of bee families overlaid on the geological column. The shaded area indicates the period of angiosperm diversification. Although flowering plants originated earlier than the shaded area indicates, the geological record does not show a dramatic increase in angiosperm diversity until when first indicated in the figure.

sent, no escape from the conclusion that bees radiated along with angiosperms in the Cretaceous.

As just discussed, bee body fossils are presently known only as far back as the Maastrichtian (Engel, 2000b). Trace fossils believed to be the product of bees are known from a variety of localities but the most notable for the discussion here are those from desposits ranging from the latest Cenomanian (Elliott and Nations, 1998) to the earliest Paleocene (e.g., Genise and Bown, 1996; Genise and Hazeldine, 1998; Genise, 1999; Genise and Verde, 2000). The depth and total number of cells in some of these nests were taken as evidence for social behavior (e.g., Elliott and Nations, 1998) but as mentioned above such attributes are not correlated with sociality in living bees and solitary bees can dig remarkably deep and large nests. It

would be impossible to state, based on nest design, whether any of these presumed tracemakers (if indeed bees) were social. The identity of most of these traces is suspect but a few—such as the ichnogenus *Uruguay* (Roselli, 1938)—are clearly the product of bee activity. Thus, trace fossils do provide some, albeit limited, information for documenting Cretaceous bees. The Late Maastrichtian (although perhaps earliest Paleocene) ichnogenus *Uruguay* is remarkably similar to cell-cluster nests of halictid bees, and those of the tribe Augochlorini in particular [this based on a cladistic reconstruction of nest architecture known for living Augochlorini Engel (1998b: also summarized briefly in Engel, 2000a), which reconstructed a groundplan design for the tribe that included cell-clusters]. Although another feature concluded to be plesiomorphic to the tribe was semisocial behavior, this determination was based merely on the distribution of sociobiological attributes of Recent species and not on correlated aspects of their nest architecture (Engel, 1998b, 2000a). At that time the augochlorines were hypothesized to be at least 75–80 Ma and to have originated from regions today in southern South America; thus, there is a tantalizing correlation between the reconstructed groundplan nest design for Augochlorini and the structure of *Uruguay.* It is possible that the tracemakers may not have been primitive Augochlorini but neither should augochlorines be excluded as a likely candidate. Genise and Verde (2000) dismissed the augochlorine hypothesis for these cells, concluding that "... *Uruguay* cannot be attributed to sweat bees because of its size, thickened walls, spiral closures and other features". In actuality, none of these can exclude the possibility of sweat bees for the following reasons: **1.** it is true that for typical sweat bees, such as *Dialictus* (tribe Gastrohalictini), the cell sizes of *Uruguay* are too large; however, the cell sizes are ample for the more robust augochlorines (e.g., *Pseudaugochlora, Megommation,* some *Augochloropsis,* some *Rhinocorynura,* &c.); moreover, several of these species are known to produce cell clusters [(of cell-cluster-producing Augochlorini, cell sizes can range from 8 mm up to at least 21 mm (Sakagami and Michener, 1962), while the range of cell sizes in *Uruguay auroranormae* Roselli are from 12–15 mm (Genise and Bown, 1996)]; **2.** the thickness of cell walls is quite variable in halictines, and the most distinct thickenening of the walls in *Uruguay* are at the cell apex, a feature typical in nests where the cells are reused; for example, in *Pseudaugochlora* where cells in a cell-cluster are reused, the bees fill in more soil mostly at the apex of the old cell and to a lesser degree on the sides before applying a new cell lining (Michener and Lange, 1958), resulting in a similar cell construction to that of the trace-fossil; and **3.** spiral closures are well known in halictines, albeit less conspicuous in some species (Sakagami and Michener, 1962). The possibility remains that *Uruguay* is the oldest evidence of sweat bee activity. If indeed the products of bees (perhaps also Halictinae), then the fossilized nests described by Elliott and Nations (1998) would be the oldest record of bees presently known (ca. 92 Ma), as well as superceding *Uruguay* as the oldest record for Halictinae. Ichnology contributes important information for understanding the evolutionary history of particular taxa. The unification of paleontology and paleoichnology will undoubtedly be increasingly important in the future for elucidating the evolution of bees (Genise and Engel, 2000).

Although the region of bee origination and diversification is speculative, the xeric interior of western Gondwanaland (southern South America, Africa, and portions of Antarctica) is most likely to have been the area from which they arose. Today, bees and spheciform wasps, particularly the basal groups of most families, are most abundant and diverse in such xeric habitats (although clear exceptions do occur in some subfamilies). This pattern of xeric-concentrated diversity is also true for the Masarinae and major pollinating flies (Gess, 1996; Grimaldi, 1999). A rudimentary cladistic reconstruction of habitat preference among bees would predict a distributional restriction to xeric regions for the ancestor of all Apiformes. This is congruent with the hypothesis that the first angiosperms were decumbent herbaceous plants (Taylor and Hickey, 1992) and that the climate in the Cretaceous was generally drier than today (Spicer et al., 1993). Flowering plants themselves likely originated (although

at an earlier date) in these xeric regions (Raven and Axelrod, 1974; Taylor and Hickey, 1992). Associating this hypothesized ancestral bee habitat with the supposed area of origination for angiosperms implicates western Gondwanaland as the most likely regional candidate. As hypothesized by Grimaldi (1999), the significant xeric diversity of pollinating insects (including bees) may represent Cretaceous "refugia". That the most plesiomorphic and presumably ancient bees of the paraphyletic subfamily Colletinae are most diverse in temperate South America and Australia is perhaps indicative of this origination in Gondwanaland (colletines are also represented in southern Africa by *Colletes* and *Scrapter,* but to a much lesser degree than elsewhere). It is perhaps also significant that many basal groups of the various families show globally disjunct or, in some cases, primarily Gondwanan distributions. For example, aside from Colletinae, there are the subfamilies of Halictidae (themselves each likely ancient) that perhaps originated early and subsequently diversified in different regions. The Andreninae are found mostly in the Laurasian continents and perhaps diversified there after having moved out of western Gondwanaland. The remaining basal subfamilies of Andrenidae and basal tribes of Panurginae are southern in distribution (the subfamily Euherbstiinae is the sole representative of non-panurgine andreninds in southern South America with Alocandreninae slightly farther north in Peru). The Panurginae are diverse in xeric regions and the Old World tribes (i.e., Panurgini, Melitturgini, and Meliturgulini) perhaps invaded through Africa during the breakup of the continents and then subsequently returned to western North America in the Tertiary (i.e., within the Panurgini). Primitive megachilids of the Fideliinae (which occur in southern South America and southern Africa except for one species in Morocco) and Xylocopinae in the Apidae also demonstrate similar patterns of diversity. These patterns, however, must be taken with caution since some of these groups may have been once more diverse than they are today. For instance, on the basis of living taxa alone, the Lithurginae, with basal living groups most diverse in temperate South America, would appear to hold this pattern. However, the most plesiomorphic lithurgine, *P. ditomeus* (see Cladistic Analyses above), is present in Baltic amber indicating extinct, basal lineages that were once more globally distributed. Extinction has certainly been a significant factor in bee evolution and must be taken into consideration when attempting to explain present day distributions (refer also to Grande, 1985; Grimaldi, 1992).

There is a possible taphonomic outcome of the original habitat preference of bees that may pose difficulties when trying to locate mid-Cretaceous fossils. If bees originated in xeric regions and subsequently invaded more forested and tropical habitats, then it may become increasingly difficult to find older bee fossils in amber since these are not the paleoenvironments thought to eventually produce amber deposits. The original bees may simply not have occurred in regions where amber was being formed. If this is the case, then there will be a heavy reliance on compression fossils for locating the earliest bees. Furthermore, the minute details needed to distinguish an early bee from a spheciform wasp would perhaps be hard to discern in a mid-Cretaceous amber inclusion. Such a distinction among taxa may be overwhelmingly difficult even in the finest of compression fossils. Therefore, it may become increasingly challenging to piece together progressively more ancient bee faunas.

How the transition from a prey-hunting spheciform wasp to vegetarian bee took place is, of course, entirely conjectural. Despite our inability to ever know how such a significant evolutionary transition might have unfolded, it is interesting to speculate on this event as well as those groundplan features most likely to have characterized the *Urbiene* or "proto-bee". Several authors have hypothesized about the traits of the "proto-bee" with varying degrees of speculation on processes (e.g., Malyshev, 1968; Radchenko and Pesenko, 1994a, 1994b, 1996; Michener, 2000a, 2000b). The following account presented herein is generally in accord with most of those prior views and I have therefore kept this discussion and my speculative scenarios to a minimum.

By undertaking a cladistic reconstruction for the Apiformes (figs. 122, 123) it is possible to obtain a generalized picture of the

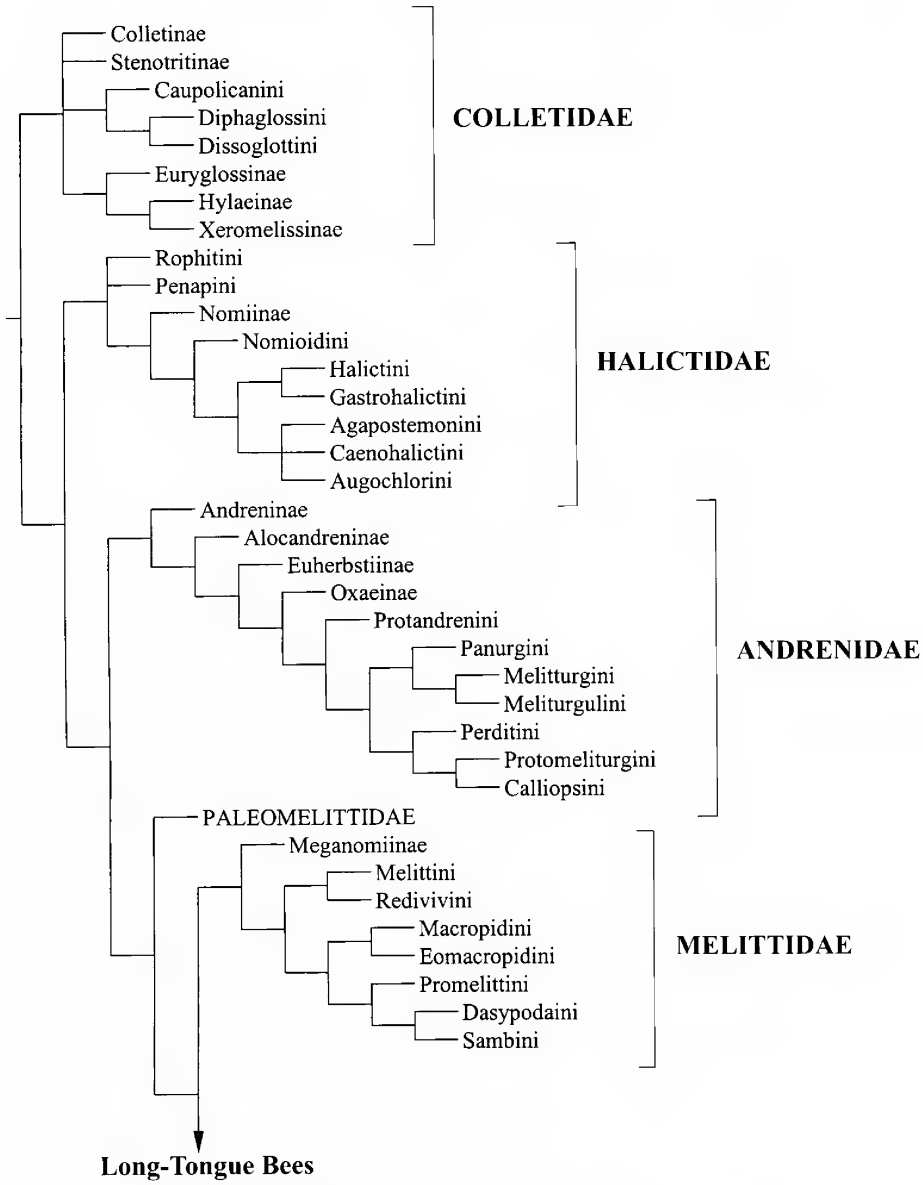


Fig. 122. Phylogeny of the bees (short-tongued bee families).

groundplan morphological and biological attributes that were likely present in the ancestor of all bees. The Colletidae are indeed the most basal family of the Apiformes (figs. 121, 122) but the clade consisting of the "wasp-like" subfamilies Hylaeinae, Euryglossinae, and Xeromelissinae is likely not to be plesiomorphic for this family nor from where groundplan traits of all bees should be sought. As alluded to above, the subfamily Colletinae as it is presently constituted is very likely paraphyletic not only to Stenotri-

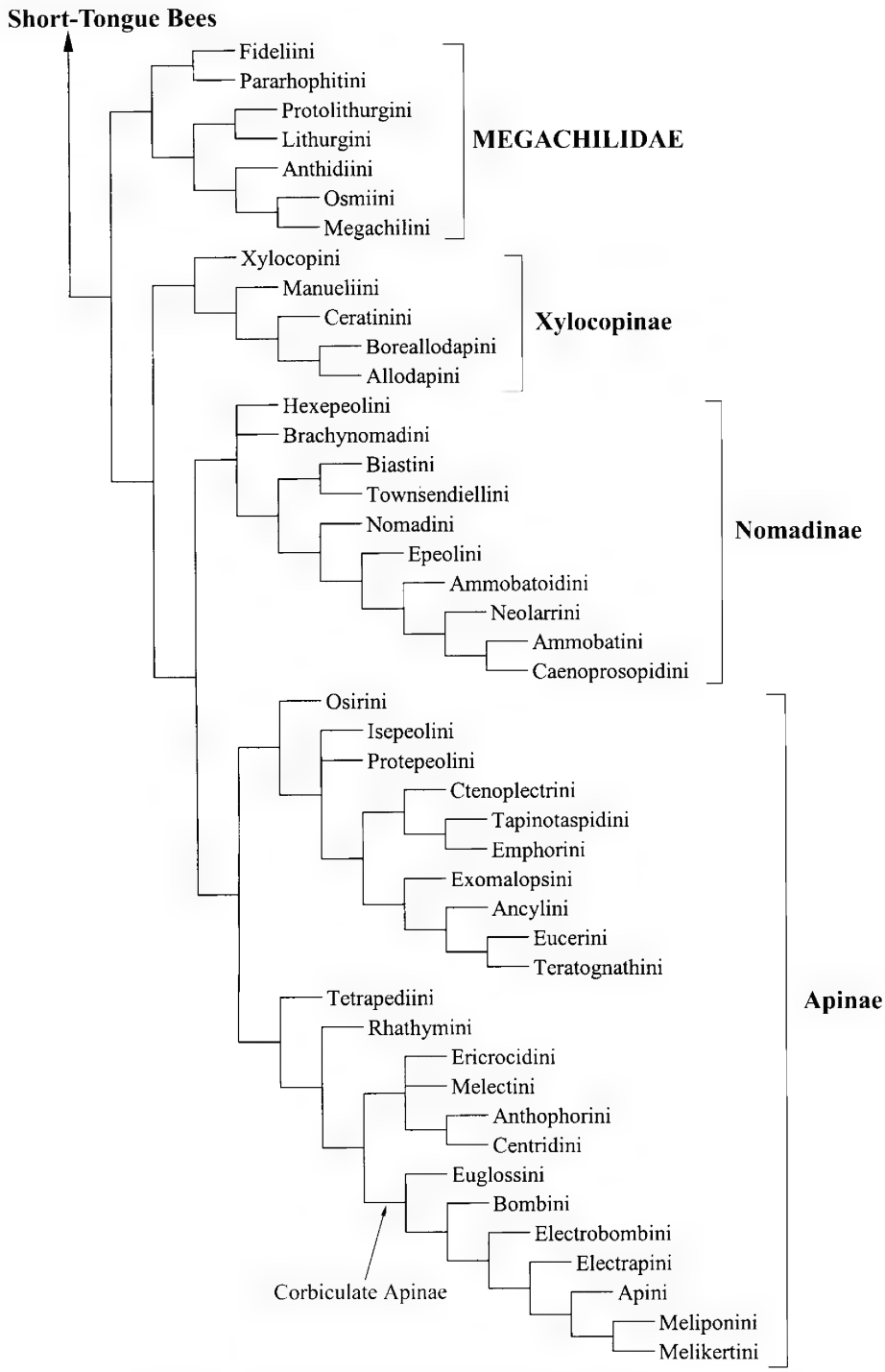


Fig. 123. Phylogeny of the bees (long-tongued bee families).

tinae and Diphaglossinae but also to the Hylaeinae + Euryglossinae + Xeromelissinae clade. Presently, relationships among the several genera of Colletinae are not entirely clear so I have avoided splitting the subfamily apart for the time being. Some genera, such as *Scrapter* and *Callomelitta,* may prove to be more closely related to the latter three subfamilies as well as *Colletes,* while the stenotritines may be sister to a clade of Australian colletines (e.g., some Paracolletini), thereby rendering Colletinae with its current composition paraphyletic to all other colletids (see also McGinley, 1981). The internal phylogeny of Colletidae, however, is in need of clarification and any discussion (including the one presented herein) of the "proto-bee" must be considered as tentative. By this account, however, the general wasp-like features of hylaeines and euryglossines (e.g., reduced scopae) are apomorphic for this colletid clade and not plesiomorphic for bees. Thus, groundplan features for the bees should be derived from plesiomorphic traits of the Colletinae, Halictidae, and Andrenidae as well as the remaining families. From these considerations the "proto-bee" was a relatively robust, moderately pubescent, short-tongued apoid with a broad glossa. Pollen would have been carried externally on the body and not within the crop (as is done by species of Hylaeinae and Euryglossinae). Ground-nesting is a groundplan feature of each family and thereby of the bees as a whole; the "proto-bee" would have therefore constructed simple burrows in the soil. The stem-group wasps from which the "proto-bee" itself arose would have nested in the soil (such a reconstruction based on the features of the spheciform wasps is well supported). Such wasps would perhaps have brought back pollen-covered prey that females had captured on early flowering plants. Once the wasp larva had by chance become able to digest and make use of the pollen as a protein resource, it was perhaps not long before pollen became the primary, if not sole, source of food. A female wasp would have a decreased search-time for provisions owing to the fact that flowers advertise themselves for pollination and are stationary while prey attempt to hide and are mobile. Moreover, negative consequences such as injury and risk of death to the provisioning female from those prey that might fight back would be immediately given up. Such presumably strong selective pressures in this scenario would quickly result in any such lineage of wasps to become vegetarian. The plumose setae, a distinguishing trait of bees, were likely not an original adaptation for the transport of pollen. Plumose setae were perhaps, as discussed by Michener (2000a), a means of conserving water in an arid environment. Branched setae are not a necessity for the transport of pollen since many bees have simple scopal setae. As mentioned above, bees likely arose in the xeric interior of Gondwanaland and plumose setae would potentially have been a novel mechanism for decreasing integumental evaporation (in contrast to simply increasing the total number of setae). As also pointed out by Michener (2000a), that such setae are generally pale (white or off-white) and are a groundplan feature for the bees is also suggestive since many xeric-environment insects presumably use pale hue to reflect heat and as protective coloration. As just mentioned, pilosity serves a thermoregulatory function (e.g., Church, 1960). In hovering and other strong flying, pollinating insects, like bees and beeflies, thick pilosity also serves to maintain a high body temperature, especially as flight begins after torpor from cold, desert nights. Clearly, some desert bees have minimal setae (e.g., some *Xylocopa*) but those that fly earlier in the morning tend to be more setose. Plumose setae in the "proto-bee" likely played a role in thermoregulation and water conservation rather than in pollen transport.

The major lineages of bees (i.e., families, perhaps some subfamilies) perhaps diversified rapidly shortly following the origin of bees as a whole (figs. 121–123). The division into those ancestral lineages that eventually gave rise to the various families recognized today must have taken place sometime between 125–90 Ma. These families then progressed along independent evolutionary tracks, undoubtedly with numerous groups that exhibited interesting character combinations becoming extinct at various stages (and as is documented above, several by the latest Eocene at least since only modern groups are known in the Oligocene and

younger deposits), leaving the six families we recognize today. The family Paleomelittidae represents one such "intermingled" lineage whose extinction left large character gaps between the surviving lineages. Such extinct lineages were perhaps dwindling by middle Eocene times. At present there should be little or no concern for the absence of a tight correlation between the stratigraphic ranks and phylogenetic ranks of bee taxa. Significant correlations have been found in a variety of taxa where the fossil record is relatively well represented and cladograms are well resolved (e.g., Norell and Novacek, 1992a, b; Borkent, 1995; Grimaldi and Cumming, 1999). For the bees, however, the fossil record is comparatively sparse, with geological data points based on limitations: **1.** in number of well preserved specimens upon which to base character analyses; **2.** in chronological diversity and number of horizons with identifiable bee specimens (only a few, scattered deposits have at present revealed fossil bees); **3.** in diversity and number of higher-level lineages (e.g., tribes) with a fossil record of any sort [e.g., see appendix 2, where of 83 suprageneric groups (not including subtribes) only 28 are represented in the fossil record, and most of these are based on dubiously assigned compression fossils (personal obs.)]; and **4.** in number of cladistic analyses for bee groups.

Although bees are quite rare as amber inclusions (except for the common *Proplebeia dominicana* in Dominican amber), the exploration of Cretaceous amber sites for older bees is imperative, no matter how seemingly futile. Compression fossils will also play an important, albeit somewhat more limited, role in understanding bee evolution and may eventually prove to be critical for understanding the earliest of bees. Such exploration of the Cretaceous will hopefully bring to science additional lineages that close the gaps in our knowledge and help us to further refine the scenario of bee diversification I have presented. It is from such Mesozoic fossils (particularly those preserved in amber) that the greatest contributions will come for not only understanding bee origins but for reconstructing the pattern of bee phylogeny.

The Eocene Bee Fauna

A general pattern of affinity between the Eocene fauna of Europe and the present day faunas of Asia and sub-Saharan Africa is documented for various groups (e.g., Ander, 1942; Larsson, 1978). For example, the famous Baltic amber lizard has affinities to groups in Africa and was even assigned, until recently, to the living African genus *Nucras* (Böhme and Weitschat, 1998). Likewise, the Baltic amber scorpion *Palaeolychras balticus* Lourenço and Weitschat has as its nearest relative a genus presently occurring in Africa and southern Asia (Lourenço and Weitschat, 1996). A similar pattern certainly holds true for the Baltic amber bees. The Boreallodapini is allied to the Allodapini, a tribe that has its greatest diversity in sub-Saharan Africa, southeast Asia, and Australia (see also discussion above under Cladistic Analyses). The genera *Kelneriapis, Liotrigonopsis,* and *Electrolictus* are all most similar and certainly related to genera today occurring in Africa and southeast Asia (namely *Hypotrigona, Liotrigona,* and *Patellapis,* respectively). Similarly, the Melikertini is sister to Meliponini, a group that is today pantropical in distribution and the Glyptapina have affinities with the Old World (principally African) Anthidiini.

The bee fauna of the Baltic amber is unique, with a wider array of bees than any other Lagerstätte in the world. The fauna is further important for the preservation of a number of primitive, higher groups that failed to survive to the present day. This is in sharp contrast to younger fossil faunas from the Oligocene or Miocene where species belong to extant genera or extinct genera closely related to modern groups and in all cases to living tribes, subfamilies, and families (e.g., lowest Miocene Dominican amber: table 1; Oligocene of Germany: Engel, 1998c). It is possible that some of the extinct lineages from the Baltic amber fauna are the final Tertiary survivors of originally Mesozoic bee lineages. Owing to the presence of a meliponine in latest Cretaceous amber (Engel, 2000b), this is almost certainly the case for the tribes Electrobombini, Electrapini, and Melikertini as well as the Paleomelittidae. The almost modern character of the only

halictine in the Baltic amber fauna, *Electrolictus,* is indicative of not only this tribe's antiquity, but of that for the whole family. From the available paleomelittological information it would appear that the bees underwent at least two periods of diversification. The first was either at their origin or shortly thereafter and produced the array of taxa that eventually gave rise to families we recognize today. The second radiation appears to have been in the Tertiary. As mentioned repeatedly above, those taxa from the Eocene and earlier all belong to extinct genera and, where information is available, most belong to higher categories (i.e., tribes, subfamilies, and families) that are no longer extant. Immediately following the Eocene and by the earliest Miocene the bee fauna becomes remarkably modern in appearance, with most fossils belonging to living genera. There are no extinct suprageneric lineages in Oligocene or younger deposits. The bees in the Eocene and perhaps older deposits were presumably remnants of originally Cretaceous diversifications. At the end of the Eocene those enigmatic higher lineages were perhaps dwindling and, at least in Europe, their eventual disappearance was possibly aided by the changing global climate at the time. Thus, at the Eocene-Oligocene transition there was a dramatic shift in the tribal composition of the bee fauna to entirely modern tribes and essentially modern genera that either originated or first experienced their greatest radiation at that time. Thus, the bee fauna we are familiar with today appears to have had its compositional origin in the Oligocene Epoch.

It is significant that there is such a remarkable diversity of advanced eusocial corbiculate bees in the Eocene fauna and more so that most of these taxa represent higher lineages that have since become extinct (Engel, in press-b). A general, epoch-by-epoch overview of the geological history of the corbiculate Apinae (e.g., Engel, 2000c) shows a decrease in diversity at higher categorical levels (e.g., genera and tribes), particularly between the Eocene and Oligocene Epochs. During this transition period numerous tribes and genera of advanced eusocial lineages disappeared so that by the Oligocene the corbiculate bee fauna was essentially modern in character and, in fact, the bee fauna as a whole became very modern at this period. This is noteworthy since the success, as measured by ecological dominance and specific diversity, of groups such as the termites (ca. 3,000 species), ants (ca. 16,000 species), and social wasps (ca. 1,000 species) has been directly attributed to their advanced eusocial behavior. The bees have been understandably included with these lineages since bees are undoubtedly more diverse than all three combined and arguably more ecologically dominant owing to their role as the most significant pollinators of angiosperms. Bees as a whole, however, are mostly solitary, while the advanced eusocial lineages (all restricted to the corbiculate Apinae) account for merely ca. 380 species. Not surprisingly, pollination has likely driven the overall specific diversity of bees but counter-intuitively, it appears that advanced eusocial behavior has not further fueled diversity in those lineages where it has arisen. In fact, it could even be argued that such highly organized and ecologically aggressive societies have hindered the specific diversity of the corbiculate bees over geological time. Advanced eusocial species, like the western honey bee, *Apis mellifera,* are known to influence the foraging patterns and abundance of other species through competition for resources (Eickwort and Ginsberg, 1980; Wenner and Thorp, 1994; Buchmann, 1996). The diversity of native bees has been negatively impacted, including that of other advanced eusocial lineages, in areas where *A. mellifera* has been introduced (e.g., Roubik et al., 1986; Sugden et al., 1996). This negative interaction is intense enough that extinction of stingless bee colonies was one of the predicted likely outcomes of the competitive interactions between introduced honey bees and native Meliponini (Roubik et al., 1986). Introduced honey bees not only negatively affect native bees but also nectar-feeding bird populations (Paton, 1993). Even amongst the living honey bees it has been observed that introduced populations of *A. mellifera* aggressively displace *A. cerana* (e.g., Sakagami, 1959). Interestingly, in *Apis,* the most ecologically dominant and aggressive eusocial group, the specific diversity is at its lowest for any advanced eusocial lineage (Engel, 1999c). The generally less aggressive Meliponini are not only more spe-

ciose than Apini, but the tribe is most diverse in regions where *Apis* species are not native (i.e., South and Central America). It is possible that over more expansive reaches of time such ecologically dominant foragers have had a more devastating impact on not only non-social species but also and perhaps especially on other advanced eusocial lineages that were not as efficient competitors. Certainly, extrinsic factors have played a role in the diversity and distribution of bees and continued paleontological work throughout the world will contribute to either supporting or refuting this hypothesis.

Epilogue

The study of amber inclusions allows the scientist to peer directly into past eons with far greater clarity than is possible from other kinds of fossils. In the case of the present work, these tiny bees, perhaps guards from some ancient colonies, have waited attentatively while 45 million years of history passed in review. Arriving in life-like form, surviving untold geological turmoil, these tiny mummies have opened a window onto a world since lost, utterly reshaping our knowledge of bee evolution. I must admit to sharing the sentiment expressed by Rev. Hope (1836), who, in regard to his own study of Baltic amber insects, wrote (p. 137):

> Let then the geologist boast of his Mastodon and Megatherium, his wondrous Saurian Reptiles, and numerous genera of unknown beings; the entomologist also prides himself on his Amber Insects, . . . , surpassing them in beauty and in colouring. Let the former add room to room, gallery to gallery, and fill a city with his relics and his casts, the latter may also rest contented with his stores, less bulky indeed although not less interesting. The earth is a study for them both, an inexhaustible field of inquiry, and it may be a matter of question which will most contribute to illustrate the condition and character of its earliest tenants.

Both the "Age of Dinosaurs" and "Age of Mammals", periods frequently referred to by scientists and laymen alike, are eclipsed by an Age of Insects. From the late Paleozoic to the present day, insects have dominated terrestrial and freshwater ecosystems. A paleontological perspective of insect diversity will, therefore, provide a powerful complement, if not in some instances a more significant component, to the reconstruction of ancient ecologies, patterns of evolution, and past epochs of life on Earth.

Acknowledgments

This work would not have been possible without the generous support of Robert G. Goelet, Chairman Emeritus of the AMNH Board of Trustees. I am sincerely grateful for his patronage and admirable support of collections-based research. Jerome G. Rozen, Jr., has been a close mentor and friend as well as serving as a sounding board during the past two years for ideas presented herein. Charles D. Michener continually provided support and advice; I am particularly grateful for his time and patience during my visits to discuss fossils, phylogeny, and evolutionary trends in bees. David A. Grimaldi has enthusiastically supported my work in paleoentomology, giving access to equipment, funds, and supplies, as well as providing valuable advice and friendship. Molly G. Rightmyer masterfully executed the numerous line illustrations in this monograph; her patient and meticulously careful work has greatly enhanced the presentation of this material.

My work also has been greatly facilitated by assistance and/or advice received either formally, during visits to foreign institutions, or during casual discussions from Alger G. Engel, Donna G. Engel, Hans Jahnke, Jan Koteja, Kumar Krishna, Valerie Krishna, Malcolm C. McKenna, Paul Nascimbene, Tam C. Nguyen, Michael Ohl, Erika Pietrzeniuk, Andrew J. Ross, and Wolfgang Weitschat. This monograph would have been far less fruitful had it not been for the generosity of the private collectors listed on pp. 17–18 (Material and Methods) who patiently allowed me to study their specimens; I am sincerely grateful to each. Barbara Kosmowska-Ceranowicz kindly supplied copies of her work and Wolfgang Weitschat copies of recent work on Baltic amber stratigraphy and dating; the latter also acted as courier for numerous specimens from private collections. Although I could not agree with his conclusions, I am appreciative to Stephen T. Hasiotis for generously supplying copies of his work concerning trace fossils in North America. Jörg Wunderlich, Jens von Holt, and Bernard Striebich made Baltic amber bees

available to the AMNH and myself; their support and interest was of great value. Lastly, I am thankful to Michael Ohl and his family for kindly hosting my stay in Berlin, Erika Pietrzeniuk for assistance while in the Institut für Paläontologie (Berlin), Hans Jahnke for providing lodging and assistance in the Institut und Museum für Geologie und Paläontologie (Göttingen), and to Kumar and Valerie Krishna for graciously hosting me during my stay in London. Oliver C. Phillips and Stanley Lombardo, of the University of Kansas Classics Department, kindly helped with Latin translations.

I am enormously indebted to Lee Herman, Brenda Jones, and Robert Voss for their help with the publication of my manuscript. The manuscript received critiques from David A. Grimaldi, Lee Herman, Zhiwei Liu, Charles D. Michener, Molly G. Rightmyer, Jerome G. Rozen, Jr., and two anonymous reviewers. I am grateful to each for their time and patience. Not all agreed with my conclusions and any remaining errors or peculiar interpretations are, naturally, my own.

REFERENCES

(Journal abbreviations are spelled out in appendix 4.)

Alexander, B. A.
1992. An exploratory analysis of cladistic relationships within the superfamily Apoidea, with special reference to sphecid wasps (Hymenoptera). J. Hym. Res. 1: 25–61.

Alexander, B. A., and C. D. Michener
1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 377–424.

Alexander, B. A., C. D. Michener, and A. L. Gardner
1998. Dasypodidae Börner, 1919 (Insecta, Hymenoptera): Proposed emendation of spelling to Dasypodaidae, so removing the homonymy with Dasypodidae Gray, 1821 (Mammalia, Xenarthra). Bull. Zool. Nomencl. 55: 24–28.

Ander, K.
1942. Die Insektenfauna des baltischen Bernsteins nebst damit verknüpften zoogeographischen Problemen. Lunds Univ. Årskr., 2 Afd. 38: 1–83.

Anderson, K. B., and B. A. LePage
1995. Analysis of fossil resins from Axel Heiberg Island, Canadian Arctic. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, Resinite, and Fossil Resins: 170–192. Washington DC: Am. Chem. Soc.

Arillo, A., A. Nel, and V. M. Ortuño
1996. Two fossil bees from the Oligocene of Izarra (Alava, Spain) (Hymenoptera, Apoidea). Bull. Soc. Entomol. France 101: 59–64.

Armbruster, L.
1938. Versteinerte Honigbienen aus dem obermiocänen Randecker Maar. Arch. Bienenkd. 19: 1–48, 97–133.

Arroyo, M. T. K., P. Primack, and J. Armesto
1982. Community studies in pollination ecology in the high Andes of central Chile. 1. Pollination mechanisms and altitudinal variation. Am. J. Bot. 69: 82–97.

Bachmayer, F., N. Symeonidis, and D. Theodoropoulos
1971. Einige Insektenreste aus den Jungtertiären Süsswasserablagerungen von Kumi (Insel Euboea, Griechenland). Ann. Geol. Pays Helleniques 23: 165–174.

Bachofen-Echt, A.
1949. Der Bernstein und seine Einschlüsse. Vienna: Springer Verlag KG.

Bawa, K. S.
1990. Plant-pollinator interactions in tropical rain forests. Annu. Rev. Ecol. Syst. 21: 399–422.

Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville, and M. H. Grayson
1985. Reproductive biology of tropical lowland rain forests. II. Pollination systems. Am. J. Bot. 72: 346–351.

Beck, C. W.
1986. Spectroscopic investigations of amber. Appl. Spectrosc. Rev. 22: 57–110.

Beck, C. W., E. Wilbur, and S. Meret
1964. Infrared spectra and the origin of amber. Nature 201: 256–257.

Beck, C. W., E. Wilbur, S. Meret, D. Kossove, and K. Kermani
1965. The infrared spectra of amber and the identification of Baltic amber. Archaeometry 8: 96–109.

Bischoff, H.
1927. Biologie der Hymenopteren: Eine Naturgeschichte der Hautflügler. Berlin: Springer Verlag.

Böhme, W., and W. Weitschat
1998. Redescription of the Eocene lacertid lizard *Nucras succinea* Boulenger, 1917 from Baltic amber and its allocation to

Succinilacerta n.gen. Mitt. Geol.-Paläontol. Inst. Univ. Hambg. 81: 203–222.

Borkent, A.
1995. Biting Midges in the Cretaceous Amber of North America (Diptera: Ceratopogonidae). Leiden: Backhuys.

Börner, C.
1919. Stammesgeschichte der Hautflügler. Biol. Zentbl. 39: 145–186.

Bour, R., and A. Dubois
1984. Nomenclature ordinale et familiale des tortues (Reptilia). Stud. Geol. Salmanticensia (Stud. Palaeochelonio1.) 1: 77–86.

Brischke, D.
1886. Die Hymenopteren des Bernsteins. Schr. Naturf. Gesell. Danzig 6: 278–279.

Brothers, D. J.
1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kansas Sci. Bull. 50: 483–648.
1976. Modifications of the metapostnotum and origin of the "propodeal triangle" in Hymenoptera Aculeata. Syst. Entomol. 1: 177–182.
1999. Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea). Zool. Scr. 28: 233–249.

Brothers, D. J., and J. M. Carpenter
1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). J. Hym. Res. 2: 227–304.

Buchmann, S. L., and G. P. Nabhan
1996. The Forgotten Pollinators. Washington DC: Island Press.

Burmeister, H.
1831. Handbuch der Entomologie: Erste Band: Allgemeine Entomologie. Berlin: G. Reimer.
1832. A Manual of Entomology. London: E. Churton. [Translation of Burmeister, 1831]

Burnham, L.
1978. Survey of social insects in the fossil record. Psyche 85: 85–133.

Buttel-Reepen, H., von
1906. Apistica. Beiträge zur Systematik, Biologie, sowie zur geschichtlichen und geographischen Verbreitung der Honigbiene (*Apis mellifica* L.), ihrer Varietäten und der überigen *Apis*-Arten. Mitt. Zool. Mus. Berl. 3: 117–201.

Camargo, J. M. F., and D. W. Roubik
1991. Systematics and bionomics of the apoid obligate necrophages: The *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). Biol. J. Linn. Soc. 44: 13–39.

Camargo, J. M. F., W. E. Kerr, and C. R. Lopes
1967. Morfologia externa de *Melipona* (*Melipona*) *marginata* Lepeletier (Hymenoptera: Apoidea). Pap. Avulsos Zool. (São Paulo) 20: 229–258.

Camargo, J. M. F., D. A. Grimaldi, and S. R. M. Pedro
2000. The extinct fauna of stingless bees (Hymenoptera: Apidae: Meliponini) in Dominican amber: Two new species and redescription of the male of *Proplebeia dominicana* (Wille and Chandler). Am. Mus. Novitates 3293: 24 pp.

Cameron, S. A.
1991. A new tribal phylogeny of the Apidae inferred from mitochondrial DNA sequences. *In* D. R. Smith (ed.), Diversity in the Genus *Apis*: 71–87. Boulder CO: Westview Press.
1993. Multiple origins of advanced eusociality in bees inferred from mitochondrial DNA sequences. Proc. Natl. Acad. Sci., U.S.A. 90: 8687–8691.

Carpenter, K.
1992. Behavior of hadrosaurs as interpreted from footprints in the "Mesaverde" Group (Campanian) of Colorado, Utah, and Wyoming. Contrib. Geol., Univ. Wyoming 1992: 81–96.

Carroll, E. J.
1962. Mesozoic fossil insects from Koonwarra, South Gippsland, Victoria. Aust. J. Sci. 25: 264–265.

Chavarría, G., and J. M. Carpenter
1994. "Total evidence" and the evolution of highly social bees. Cladistics 10: 229–258.

Church, N. S.
1960. Heat loss and body temperature of flying insects. I. Heat loss by evaporation of water from the body. II. Heat conduction within the body and its loss by radiation and convection. J. Exp. Biol. 37: 171–212.

Clark, J. M., M. A. Norell, and L. M. Chiappe
1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. Am. Mus. Novitates 3265: 36 pp.

Cockerell, T. D. A.
1906. Fossil Hymenoptera from Florissant, Colorado. Bull. Mus. Comp. Zool. 50: 33–58.

1907. A fossil honey-bee. Entomol. 40: 227–229.
1908a. Descriptions and records of bees—XIX. Ann. Mag. Nat. Hist., ser. 8, 1: 337–344.
1908b. Descriptions and records of bees—XX. Ann. Mag. Nat. Hist., ser. 8, 2: 323–334.
1908c. A fossil leaf-cutting bee. Can. Entomol. 40: 31–32.
1909a. Some European fossil bees. Entomol. 42: 313–317.
1909b. Descriptions of Hymenoptera from Baltic amber. Schr. Phys.-Ökon. Gesell. 50: 1–20.
1909c. Some additional bees from Prussian amber. Schr. Phys.-Ökon. Gesell. 50: 21–25.
1909d. Two fossil bees. Entomol. News 20: 159–161.
1909e. New North American bees. Can. Entomol. 41: 393–395.
1911a. Fossil insects from Florissant, Colorado. Bull. Am. Mus. Nat. Hist. 30: 71–82.
1911b. Descriptions and records of bees—XXXIV. Ann. Mag. Nat. Hist., ser. 8, 7: 225–237.
1913a. Some fossil insects from Florissant, Colorado. Proc. U.S. Natl. Mus. 44: 341–346.
1913b. Some fossil insects from Florissant. Can. Entomol. 45: 229–233.
1914. Miocene fossil insects. Proc. Acad. Nat. Sci., Philadelphia 66: 634–648.
1917. New Tertiary insects. Proc. U.S. Natl. Mus. 52: 373–384.
1921. Fossil arthropods in the British Museum. Ann. Mag. Nat. Hist., ser. 9, 8: 541–545.
1923. Two fossil Hymenoptera from Florissant (Vespidae, Megachilidae). Entomol. News 34: 270–271.
1925. Descriptions and records of bees—CVI. Ann. Mag. Nat. Hist., ser. 9, 16: 416–423.
1930a. The bees of Australia. Aust. Zool. 6: 205–236.
1930b. African bees of the family Ctenoplectridae from the Belgian Congo and Liberia (Hymenoptera Apoidea). Rev. Zool. Bot. Africa 18: 358–363.
1931. Insects from the Miocene (Latah) of Washington, II. Hymenoptera and Hemiptera. Ann. Entomol. Soc. Am. 24: 309–312.

Crane P. R., and S. Lidgard
1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. *In* P. D. Taylor and G. P. Larwood (eds.), Major Evolutionary Radiations: 377–407. Oxford: Clarendon Press.

Crane, P. R., E. M. Friis, and K. R. Pedersen
1995. The origin and early diversification of angiosperms. Nature 374: 27–33.

Crepet, W. L.
1996. Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. Rev. Palaeobot. Palynol. 90: 339–359.

Crepet, W. L., and K. C. Nixon
1998. Fossil Clusiaceae from the Late Cretaceous (Turonian) of New Jersey and implications regarding the history of bee pollination. Am. J. Bot. 85: 1122–1133.

Daly, H. V., C. D. Michener, J. S. Moure, and S. F. Sakagami
1987. The relictual bee genus *Manuelia* and its relation to other Xylocopinae (Hymenoptera: Apoidea). Pan-Pac. Entomol. 63: 102–124.

Darling, D. C., and M. J. Sharkey
1990. Order Hymenoptera. *In* D. A. Grimaldi (ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bull. Am. Mus. Nat. Hist. 195: 123–153.

Donoghue, M. J., J. A. Doyle, J. Gauthier, A. G. Kluge, and T. Rowe
1989. The importance of fossils in phylogeny reconstruction. Annu. Rev. Ecol. Syst. 20: 431–460.

Eickwort, G. C.
1969. A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: Halictidae). Univ. Kansas Sci. Bull. 48: 325–524.

Eickwort, G. C., and H. S. Ginsberg
1980. Foraging and mating behavior in Apoidea. Annu. Rev. Entomol. 25: 421–446.

Eickwort, G. C., and S. F. Sakagami
1979. A classification of nest architecture of bees in the tribe Augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian nest of *Rhinocorynura inflaticeps*. Biotropica 11: 28–37.

Eldredge, N., and M. J. Novacek
1985. Systematics and paleontology. Paleobiology 11: 65–74.

Elliott, D. K., and J. D. Nations
1998. Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, northeastern Arizona. Ichnos 5: 243–253.

Engel, M. S.
1995. *Neocorynura electra,* a new fossil bee species from Dominican amber (Hymenoptera: Halictidae). J. New York Entomol. Soc. 103: 317–323. [Publ. date: 5 November 1996]
1996. New augochlorine bees (Hymenoptera: Halictidae) in Dominican amber, with a brief review of fossil Halictidae. J. Kansas Entomol. Soc., Suppl. 69: 334–345. [Publ. date: 15 January 1997]
1998a. A new species of the Baltic amber bee genus *Electrapis* (Hymenoptera: Apidae). J. Hym. Res. 7: 94–101.
1998b. Phylogeny, classification, and evolutionary ethology of the bee tribe Augochlorini (Hymenoptera: Halictidae). Ph.D. diss., Cornell Univ., Ithaca, NY.
1998c. Fossil honey bees and evolution in the genus *Apis* (Hymenoptera: Apidae). Apidologie 29: 265–281.
1998d. Comparative morphology and the phylogeny of the corbiculate bees (Hymenoptera: Apidae; Apinae). Proc. 13th Intl. Congr. IUSSI, Adelaide 1998: 151.
1999a. *Apis proava* Menge, 1856 (currently *Electrapis proava*; Insecta, Hymenoptera): Proposed conservation by designation of a neotype. Bull. Zool. Nomencl. 56: 134–135.
1999b. The first fossil *Euglossa* and phylogeny of the orchid bees (Hymenoptera: Apidae; Euglossini). Am. Mus. Novitates 3272: 14 pp.
1999c. The taxonomy of recent and fossil honey bees (Hymenoptera: Apidae; *Apis*). J. Hym. Res. 8: 165–196.
1999d. *Megachile glaesaria,* the first megachilid bee fossil from amber (Hymenoptera: Megachilidae). Am. Mus. Novitates 3276: 13 pp.
1999e. Augochlorini Beebe, 1925 (Insecta, Hymenoptera): Corrected authorship and date (not Moure, 1943). Bull. Zool. Nomencl. 56: 198.
1999f. A new xeromelissine bee in Tertiary amber of the Dominican Republic (Hymenoptera: Colletidae). Entomol. Scand. 30: 453–458. [Publ. date: January 2000]
2000a. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). Bull. Am. Mus. Nat. Hist. 250: 90 pp.
2000b. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). Am. Mus. Novitates 3296: 11 pp.
2000c. Fossils and phylogeny: A paleontological perspective on social bee evolution. *In* M.M.G. Bitondi and K. Hartfelder (eds.), Anais do IV Encontro Sobre Abelhas: 217–224. Ribeirão Preto: Universidade de São Paulo.
In press-a. The first large carpenter bee from the Tertiary of North America, with a consideration of the geological history of Xylocopinae (Hymenoptera: Apidae). Trans. Am. Entomol. Soc.
In press-b. Monophyly and extensive extinction of advanced eusocial bees: Insights from an unexpected Eocene diversity. Proc. Natl. Acad. Sci., U.S.A.

Engel, M. S., and M. G. Rightmyer
2000. A new augochlorine bee species in Tertiary amber from the Dominican Republic (Hymenoptera: Halictidae). Apidologie 31: 431–436.

Engel, M. S., and T. R. Schultz
1997. Phylogeny and behavior in honey bees (Hymenoptera: Apidae). Ann. Entomol. Soc. Am. 90: 43–53.

Epis, R. C., and C. E. Chapin
1974. Stratigraphic nomenclature of the Thirtynine Mile volcanic field, central Colorado. U.S. Geol. Surv. Bull., Washington 1395-C.

Foord, A. S.
1890. Note on a collection of east coast amber belonging to Mrs. Burwood of Yarmouth. Trans. Norfolk Norwich Nat. Soc. 5: 92–95.

Friese, H.
1903. Neue Meliponiden II. Z. Syst. Hym. Dipt. 3: 359–361.

Gauthier, J., A. G. Kluge, and T. Rowe
1989. Amniote phylogeny and the importance of fossils. Cladistics 4: 105–209.

Genise, J. F.
1999. Fossil bee cells from the Asencio Formation (Late Cretaceous-Early Tertiary) of Uruguay, South America. Proc. First Intl. Palaeoentomol. Conf., Moscow 1998: 27–32.

Genise, J. F., and T. M. Bown
1996. *Uruguay* Roselli 1938 and *Roselli-chnus,* n. ichnogenus: two ichnogenera for clusters of fossil bee cells. Ichnos 4: 199–217.

Genise, J. F., and M. S. Engel
2000. The evolutionary history of sweat bees (Hymenoptera: Halictidae): Integration of paleoentomology, paleoichnology,

and phylogeny. *In* V. M. de Godoi (ed.), International Meeting on Paleoarthropodology, Abstracts: 116–177. Ribeirão Preto: Universidade de São Paulo.

Genise, J. F., and P. L. Hazeldine
1998. The ichnogenus *Palmiraichnus* Roselli for fossil bee cells. Ichnos 6: 151–166.

Genise, J. F., and M. Verde
2000. *Corimbatichnus fernandezi*: A cluster of fossil bee cells from the Late Cretaceous–Early Tertiary of Uruguay. Ichnos 7: 115–125.

Gerlach, J.
1989. Bienen-Inklusen der Gattungen *Dasypoda, Megachile* und *Apis* im baltischen Bernstein. Münster. Forsch. Geol. Paläontol. 69: 251–260.

Germar, E. F.
1839. Die versteinerten Insecten Solenhofens. Nova Acta Leopold. (Kaiserl. Leopold.-Carol. Dtsch. Akad. Naturf.) 19: 187–222.

Gess, S.K.
1996. The Pollen Wasps: Ecology and Natural History of the Masarinae. Cambridge MA: Harvard Univ. Press.

Goloboff, P. A.
1993. NoName (NONA), version 1.5.1. Program and Documentation. Fundación e Instituto Miguel Lillo, Tucúman, Argentina.

Göppert, H. R.
1836. Fossile Pflanzenreste des Eisensandes von Aachen. Nova Acta Acad. C. Leopold.-Carol. Germ. Nat. Cur. 19: 150 pp.

Grande, L.
1985. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. Paleobiology 11: 234–243.

Grimaldi, D. A.
1992. Vicariance biogeography, geographic extinctions, and the North American Oligocene tsetse flies. *In* N. J. Novacek and Q. D. Wheeler (eds.), Extinction and Phylogeny: 178–204. New York: Columbia Univ. Press.
1995. The age of Dominican amber. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, resinite, and fossil resins: 203–217. Washington DC: Am. Chem. Soc.
1999. The co-radiations of insects and angiosperms in the Cretaceous. Ann. Missouri Bot. Gard. 86: 373–406.

Grimaldi, D., and J. Cumming
1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. Bull. Am. Mus. Nat. Hist. 239: 124 pp.

Grimaldi, D., E. Bonwich, M. Delannoy, and S. Doberstein
1994. Electron microscopic studies of mummified tissues in amber fossils. Am. Mus. Novitates 3097: 31 pp.

Griswold, T. L.
1985. A generic and subgeneric revision of the *Heriades* genus-group. Ph.D. diss., Utah State Univ., Logan, UT.

Griswold, T. L., and C. D. Michener
1997. The classification of the Osmiini of the Eastern Hemisphere (Hymenoptera, Megachilidae). J. Kansas Entomol. Soc. 70: 207–253. [Publ. date: 24 March 1988]

Hasiotis, S. [T.]
1997. Abuzz before flowers. Plateau J., Mus. North. Arizona 1: 20–27.

Hasiotis, S. T., and T. M. Demko
1996. Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau. *In* M. Morales (ed.), The continental Jurassic. Mus. North. Arizona Bull. 60: 355–370.

Hasiotis, S. T., R. F. Dubiel, and T. M. Demko
1995. Triassic hymenopterous nests: Insect eusociality predates Angiosperm plants. Rocky Mountain Sec., Geol. Soc. Am. Reg. Meeting 27: 13.

Hasiotis, S. T., R. F. Dubiel, P. T. Kay, T. M. Demko, K. Kowalska, and D. McDaniel
1998. Research update on hymenopteran nests and cocoons, Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. Natl. Park Serv., Paleontol. Res. [Tech. Rep. NPS/NRGRD/GRDTR-98/01] 3: 116–121.

Heer, O.
1849. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien: Zweite Abtheilung: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen. Neue Denkschr. Allg. Schweiz. Gesell. Ges. Natwiss. 11: 1–264.
1865. Die Urwelt der Schweiz. Zürich: Friedrich Schulthess.
1867. Fossile Hymenopteren aus Oeningen und Radoboj. Neue Denkschr. Allg. Schweiz. Gesell. Ges. Natwiss. 22: 1–42.

Hong, Y.-C.
1983. Fossil insects in the diatoms of Shanwang. Bull. Tianjin Inst. Geol. Miner. Res. 8: 1–11. [In Chinese, with English summary]
1984. New fossil insects of Laiyang Group from Laiyang Basin, Shandong Province. Prof. Pap. Stratigr. Paleontol. 11: 31–41. [In Chinese, with English summary]
1985. Fossil Insects, Scorpionids and Araneids in the Diatoms of Shanwang. Beijing: Geological Publishing House. [In Chinese, with English summary]

Hong, Y.-C., and S.-J. Miao
1992. Fossil bee [sic] and its origin with discussion on the origin of the angiosperm [sic]. Mem. Beijing Nat. Hist. Mus. 51: 1–19. [In Chinese, with English summary]

Hope, F. W.
1836. Observations on succinic insects. Trans. Entomol. Soc. London 1: 133–147.

Illiger, K.
1806. William Kirby's Familien der Bienenartigen Insekten mit Zusatzen, Nachweisungen und Bemerkungen. Mag. Insektenkd. 5: 28–175.

International Commission on Zoological Nomenclature
1993. Some bee family-group names (Insecta, Hymenoptera): Names based on *Colletes* Latreille, 1802, on *Paracolletes* Smith, 1853, on *Halictus* Latreille, 1804, on *Anthidium* Fabricius, 1804 and on *Anthophora* Latreille, 1803 given precedence over some senior names. Bull. Zool. Nomencl. 50: 85–89.
1999a. Dasypodidae Börner, 1919 (Insecta, Hymenoptera): Spelling emended to Dasypodaidae, so removing the homonymy with Dasypodidae Gray, 1821 (Mammalia, Xenarthra). Bull. Zool. Nomencl. 56: 156–157.
1999b. International Code of Zoological Nomenclature. London: International Trust for Zoological Nomenclature. [Fourth edition]
2000. *Apis proava* Menge, 1856 (currently *Electrapis proava*; Insecta, Hymenoptera): Conserved by the designation of a neotype. Bull. Zool. Nomencl. 57: 236.

Itturalde-Vinent, M. A., and R. D. E. MacPhee
1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852.
1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. Bull. Am. Mus. Nat. Hist. 238: 95 pp.

Jurine, L.
1807. Nouvelle Méthode de Classer les Hyménoptères et les Diptères, vol. 1. Genéve [Geneva]: Paschoud.

Kay, P. T., J. King, S. T. Hasiotis
1999. Petrified Forest National Park Upper Triassic trace fossils yield biochemical evidence of phylogenetic link to modern bees (Hymenoptera, Apoidea). Proc. First Intl. Palaeoentomol. Conf., Moscow 1998: 60.

Keilbach, R.
1982. Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. Dtsch. Entomol. Z. 29: 129–286.

Kelner-Pillault, S.
1969a. Abeilles fossiles ancetres des apides sociaux. Proc. VI Congr. IUSSI, Bern 1969: 85–93. [Publ. date: 15 September 1969]
1969b. Les abeilles fossiles. Dalle Mem. Soc. Entomol. Ital. 48: 519–534. [Publ. date: 30 December 1969]
1970a. L'ambre Balte et sa faune entomologique avec description de deux apoides nouveaux. Ann. Soc. Entomol. France 6: 3–24.
1970b. Une mélipone (s.l.) de l'ambre Balte (Hym. Apidae). Ann. Soc. Entomol. France 6: 437–441.
1974. État d'évolution des apides de l'ambre Balte. Ann. Soc. Entomol. France: 623–634.

Kerr, W. E., and R. A. da Cunha
1976. Taxonomic position of two fossil social bees (Apidae). Rev. Biol. Trop. 24: 35–43.

Kerr, W. E., and V. Maule
1964. Geographic distribution of stingless bees and its implications (Hymenoptera: Apidae). J. New York Entomol. Soc. 72: 2–17.

Kirby, W.
1802. Monographia Apum Angliae, or, An Attempt to Divide into their Natural Genera and Families, such Species of the Linnean Genus *Apis,* as have been Discovered in England. [2 vols.] Ipswich: White.
1837. Part IV, Insects. *In* J. Richardson, Fauna Boreali-Americana; or the Zoology of the Northern Parts of British America; Containing Descriptions of the Objects of Natural History Collected on the Late Northern Land Expeditions,

Under Command of Captain Sir John Franklin, R.N.: 1–325. London: Longman.

Kirby, W., and W. Spence
1826. An Introduction to Entomology, vol. 3. London: Longman.

Kohring, R., and T. Schlüter
1989. Historische und paläontologische Bestandsaufnahme des Simetits, eines fossilen Harzes mutmäßlich mio/pliozänen Alters aus Sizilien. Doc. Nat. 56: 33–58.

Kosmowska-Ceranowicz, B.
1987. Charakterystyka mineralogiczno-petrograficzna bursztynonośnych osadów Eocenu w okolicach Chłapowo oraz osadów Paleogenu Połnocnej Polski. Biul. Inst. Geol. 356: 29–50.

Kosmowska-Ceranowicz, B., and C. Müller
1985. Lithology and calcareous nannoplankton in amberbearing Tertiary sediments from boreholes Chłapowo (Northern Poland). Bull. Pol. Acad. Sci. 33: 119–128.

Koulianos, S., R. Schmid-Hempel, D. W. Roubik, and P. Schmid-Hempel
1999. Phylogenetic relationships within the corbiculate Apinae (Hymenoptera) and the evolution of eusociality. J. Evol. Biol. 12: 380–384.

Lambert, J. B., J. S. Frye, and G. O. Poinar, Jr.
1985. Amber from the Dominican Republic: Analysis by nuclear magnetic resonance spectroscopy. Archaeometry 27: 43–51.

Langenheim, J. H.
1969. Amber: A botanical inquiry. Science 163: 1157–1169.

Lanham, U. N.
1979. Possible phylogenetic significance of complex hairs in bees and ants. J. New York Entomol. Soc. 87: 91–94.
1980. Evolutionary origin of bees (Hymenoptera: Apoidea). J. New York Entomol. Soc. 88: 199–209.

Larsson, S. G.
1978. Baltic Amber—A Paleobiological Study. Klampenborg: Scandinavian Science Press.

Latreille, P. A.
1802a. Histoire Naturelle des Fourmis, et Recueil de Mémoires et d'Observations sur les Abeilles, les Araignées, les Faucheurs, et Autres Insectes. Paris: Crapelet.
1802b. Histoire Naturelle Générale et Particulière des Crustacés et des Insectes, Tome 3. Paris: Dufart.
1804. Tableau méthodique des insectes. *In* Nouveau Dictionnaire d'Histoire Naturelle, Appliquée aux Arts, Principalement à l'Agriculture et à l'Economie Rurale et Domestique, Tome 24, Charactères et Tables: 129–200. Paris: Deterville.
1809. Genera Crustaceorum et Insectorum Secundum Ordinem Naturalem in Familias Disposita, Iconibus Exemplisque Plurimis Explicata, Tome 4. Paris: Koenig.

Lepeletier de Saint Fargeau, A. L. M.
1836. Histoire Naturelle des Insectes—Hyménoptères, Tome 1. Paris: Roret.

Lidgard, S., and P. R. Crane
1988. Quantitative analyses of the early angiosperm radiation. Nature 331: 344–346.

Linnaeus, C. [Linné, K., von]
1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, vol. 1, ed. 10, Reformata. Holmiae [Stockholm]: Salviae.

Lockley, M. G., and M. Matsukawa
1999. Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs. Palaeogeogr., Palaeoclimatol., Palaeoecol. 150: 25–31.

Lomholdt, O.
1982. On the origin of the bees (Hymenoptera: Apidae, Sphecidae). Entomol. Scand. 13: 185–190.

Lourenço, W. R., and W. Weitschat
1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion *Tityus eogenus* Menge, 1869 can finally be clarified. Mitt. Geol.–Paläontol. Inst. Univ. Hambg. 79: 183–193.

Lutz, H.
1993. *Eckfeldapis electrapoides* nov. gen. n. sp., eine "Honigbiene" aus dem Mittel-Eozän des "Eckfelder Maares" bei Manderscheid/Eifel, Deutschland (Hymenoptera: Apidae, Apinae). Mainzer Natwiss. Arch. 31: 177–199.

Malyshev, S. I.
1968. Genesis of the Hymenoptera and the Phases of their Evolution. London: Methuen.

Manning, F. J.
1960. A new fossil bee from Baltic amber. Verh. XI Intl. Kongr. Entomol., Wien 1: 306–308. [Publ. date: 1961]

Mardulyn, P., and S. A. Cameron
1999. The major opsin in bees (Insecta: Hymenoptera): A promising nuclear gene for higher level phylogenetics. Mol. Phylogenet. Evol. 12: 168–176.
McGinley, R. J.
1981. Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae (Hymenoptera: Apoidea). Univ. California Publ. Entomol. 91: 1–307.
McKenna, M. C.
1975. Fossil mammals and early Eocene North Atlantic land continuity. Ann. Missouri Bot. Gard. 62: 335–353.
McKenna, M. C., and S. K. Bell
1997. Classification of Mammals Above the Species Level. New York: Columbia Univ. Press.
Melo, G. A. R.
1999. Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. Univ. Kansas Nat. Hist. Mus. Sci. Pap. 14: 1–55.
Menge, A.
1856. Lebenszeichen vorweltlicher, im Bernstein eingeschlossener Thiere. Danzig: Kafemann.
Michener, C. D.
1941. A generic revision of the American Osmiini with descriptive notes on Old World genera. Am. Midl. Nat. 26: 147–166.
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Am. Mus. Nat. Hist. 82: 151–326.
1965. A classification of the bees of the Australian and South Pacific regions. Bull. Am. Mus. Nat. Hist. 130: 1–362.
1977. Discordant evolution and the classification of allodapine bees. Syst. Zool. 26: 32–56.
1978. The classification of halictine bees: Tribes and Old World nonparasitic genera with strong venation. Univ. Kansas Sci. Bull. 51: 501–538.
1979. Biogeography of the bees. Ann. Missouri Bot. Gard. 66: 277–347.
1981a. Comparative morphology of the middle coxae of Apoidea. J. Kansas Entomol. Soc. 54: 319–326.
1981b. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contrib. Am. Entomol. Inst. 18: 1–135.
1982. A new interpretation of fossil social bees from the Dominican Republic. Sociobiol. 7: 37–45.
1983. The classification of the Lithurginae (Hymenoptera: Megachilidae). Pan-Pac. Entomol. 59: 176–187.
1986. Family-group names among bees. J. Kansas Entomol. Soc. 59: 219–234.
1990. Classification of the Apidae (Hymenoptera). Univ. Kansas Sci. Bull. 54: 75–164.
1991. Proposed precedence of some bee family-group names (Insecta, Hymenoptera): Names based on *Colletes* Latreille, 1802, on *Paracolletes* Smith, 1853, on *Halictus* Latreille, 1804, on *Anthidium* Fabricius, 1804 and on *Anthophora* Latreille, 1803 to have precedence over some senior names. Bull. Zool. Nomencl. 48: 227–235.
1997. Genus-group names of bees and supplemental family-group names. Univ. Kansas Nat. Hist. Mus. Sci. Pap. 1: 1–81.
1999. The corbiculae of bees. Apidologie 30: 67–74.
2000a. The Bees of the World. Baltimore MD: Johns Hopkins Univ. Press.
2000b. What was the proto-bee? *In* M.M.G. Bitondi and K. Hartfelder (eds.), Anais do IV Encontro Sobre Abelhas: 2–8. Ribeirão Preto: Universidade de São Paulo.
Michener, C. D., and R. W. Brooks
1984. Comparative study of the glossae of bees (Apoidea). Contrib. Am. Entomol. Inst. 22: 1–73.
Michener, C. D., and A. Fraser
1978. A comparative anatomical study of mandibular structure in bees. Univ. Kansas Sci. Bull. 51: 463–482.
Michener, C. D., and L. Greenberg
1980. Ctenoplectridae and the origin of long-tongued bees. Zool. J. Linn. Soc. 69: 183–203.
Michener, C. D., and D. A. Grimaldi
1988a. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). Am. Mus. Novitates 2917: 10 pp.
1988b. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. Proc. Natl. Acad. Sci., U.S.A. 85: 6424–6426.

Michener, C. D., and T. L. Griswold
1994. The classification of Old World Anthidiini (Hymenoptera, Megachilidae). Univ. Kansas Sci. Bull. 55: 299–327.
Michener, C. D., and R. B. Lange
1958. Observations on the behavior of Brasilian halictid bees, III. Univ. Kansas Sci. Bull. 39: 473–505.
Michener, C. D., and G. O. Poinar, Jr.
1996. The known bee fauna of the Dominican amber. J. Kansas Entomol. Soc., Suppl. 69: 353–361. [Publ. date: 15 January 1997]
Michener, C. D., and J. G. Rozen, Jr.
1999. A new ground-nesting genus of xeromelissine bees from Argentina and the tribal classification of the subfamily (Hymenoptera: Colletidae). Am. Mus. Novitates 3281: 10 pp.
Minckley, R. L.
1998. A cladistic analysis and classification of the subgenera and genera of the large carpenter bees, tribe Xylocopini (Hymenoptera: Apidae). Univ. Kansas Nat. Hist. Mus. Sci. Pap. 9: 1–47.
Moldenke, A. R.
1976. California pollination ecology and vegetation types. Phytologia 34: 305–361.
Motschulsky, V., de
1856. Voyages. Lettres de M. de Motschulsky à M. Ménétriés. Etude Entomol. 5: 3–38.
Moure, J. S.
1946. Melíponas do Brasil. Chácaras Quint. (São Paulo) 74: 609–612.
1949. Las especies chilenas de la sub-familia Lithurginae (Hym.—Apoidea). Arq. Mus. Parana. 7: 265–286.
1961. A preliminary supra-specific classification of the Old World meliponine bees (Hym., Apoidea). Stud. Entomol. 4: 181–242.
Moure, J. S., and J. M. F. Camargo
1978. A fossil stingless bee from copal (Hymenoptera: Apidae). J. Kansas Entomol. Soc. 51: 560–566. [Publ. date: 17 November 1978]
Moure, J. S., and C. D. Michener
1955. The bee family Fideliidae in South America (Hymenopt.—Apoidea). Dusenia 6: 199–206.
Müller, H.
1872. Anwendung der Darwinschen Lehre auf Bienen. Verh. Naturhist. Ver. Preuss. Rheinlande Westphalen 29: 1–96.
Nascimbene, P., and H. Silverstein
2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. *In* D. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey: 93–102. Leiden: Backhuys.
Newman, E.
1834. Attempted division of British insects into natural orders. Entomol. Mag. 2: 379–431.
Nixon, K. C.
1999. WINCLADA, version 0.9.99tuc.13, beta. Program and Documentation, Cornell Univ., Ithaca, NY.
Nixon, K. C., and J. M. Carpenter
1996. On consensus, collapsibility, and clade concordance. Cladistics 12: 305–321.
Noll, F. B.
1998. Are behavioral characters informative of phylogenetic relationships among the corbiculate bees (Hymenoptera, Apidae, Apinae). Proc. 13th Intl. Congr. IUSSI, Adelaide 1998: 347.
Norell, M. A., and M. J. Novacek
1992a. The fossil record and evolution: Comparing cladistic and paleontologic evidence for vertebrate history. Science 255: 1690–1693.
1992b. Congruence between superpositional and phylogenetic patterns: Comparing cladistic patterns with fossil records. Cladistics 8: 319–337.
Norell, M. A., J. M. Clark, L. M. Chiappe, and D. Dashzeveg
1995. A nesting dinosaur. Nature 378: 774–776.
Novacek, M. J., and Q. D. Wheeler
1992. Extinction and Phylogeny. New York: Columbia Univ. Press.
Novak, O.
1877. Fauna der Cyprisschiefer des Egerer Tertiärbeckens. Sitzungsber. Akad. Wiss. Wien, Math.-Natwiss. Kl. 76: 71–96.
Olfers, E., von
1907. Die "Ur-Insekten" (Thysanura und Collembola) im Bernstein. Schr. Phys.-Ökon. Gesell. 48: 1–40.
Ornduff, R.
1991. Size classes, reproductive behavior, and insect associates of *Cycas media* (Cycadaceae) in Australia. Bot. Gaz. 152: 203–207.

Panzer, G. W. F.
1806. Kritische Revision der Insektenfauna Deutschlands, vol. 2. Nürnberg: Felssecker.
1809. Faunae Insectorum Germanicae Initia oder Deutschlands Insecten, Heft 107. Nürnberg: Felssecker.
Patiny, S.
1999. Etude phylogénétique des Panurginae de l'ancien monde (Hymenoptera, Andrenidae). Linzer Biol. Beitr. 31: 249–275.
Paton, D. C.
1993. Honeybees in the Australian environment. Bioscience 43: 95–103.
Patterson, C.
1981. Significance of fossils in determining evolutionary relationships. Annu. Rev. Ecol. Syst. 12: 195–223.
Pesenko, Yu. A.
1983. Fauna of the U.S.S.R., Hymenopteran Insects, Vol. 17, Nr. 1, Halictid Bees (Halictidae), Subfamily Halictinae, Tribe Nomioidini (in the Palaearctic Fauna). Leningrad [St. Petersburg]: Zool. Inst., Acad. Sci. [In Russian]
1999. Phylogeny and classification of the family Halictidae revised (Hymenoptera: Apoidea). J. Kansas Entomol. Soc. 72: 104–123. [Publ. date: 19 January 2000]
Pesenko, Yu. A., J. Banaszek, V. G. Radchenko, and T. Cierzniak
2000. Bees of the Family Halictidae (Excluding *Sphecodes*) of Poland: Taxonomy, Ecology, Bionomics. Bydgoszcz: Pedagogical Univ.
Petanidou, T., and D. Vokou
1990. Pollination and pollen energetics in Mediterranean ecosystems. Am. J. Bot. 77: 986–992.
Petrov, P.
1992. Distribution and phylogenesis of the bee genus *Apis* (Hymenoptera, Apidae). Usp. Sovrem. Biol., Moscow 112: 359–372. [In Russian]
Pielinska, A.
1997. Inclusions of wood in the amber collections of the Museum of the Earth in Warsaw. Metalla, Bochum 66: 25–28.
Piton, L.-E.
1940. Paléontologie du Gisement Éocène de Menat (Puy-de-Dôme) (Flore et Faune). Paris: Lechevalier.
Poinar, G. O., Jr.
1991. *Praecoris dominicana* gen. n., sp. n. (Hemiptera: Reduviidae: Holoptilinae) from Dominican amber, with an interpretation of past behavior based on functional morphology. Entomol. Scand. 22: 193–199.
1994. Bees in fossilized resin. Bee World 75: 71–77.
1998. *Paleoeuglossa melissiflora* gen. n., sp. n. (Euglossinae: Apidae), fossil orchid bees in Dominican amber. J. Kansas Entomol. Soc. 71: 29–34. [Publ. date: 9 February 1999]
Poinar, G. O., Jr., and J. Haverkamp
1985. Use of pyrolysis mass spectroscopy in the identification of amber samples. J. Baltic Stud. 16: 210–221.
Prentice, M.
1991. Morphological analysis of the tribes of Apidae. *In* D. R. Smith (ed.), Diversity in the genus *Apis*: 51–69. Boulder CO: Westview Press.
Proctor, M., P. Yeo, and A. Lack
1996. The natural History of Pollination. Portland OR: Timber Press.
Prothero, D. R.
1994. The Eocene-Oligocene Transition: Paradise Lost. New York: Columbia Univ. Press.
Radchenko, V. G., and Yu. A. Pesenko
1994a. "Protobee" and its nests: A new hypothesis concerning the early evolution of Apoidea (Hymenoptera). Entomol. Obozr. 73: 913–933. [In Russian]
1994b. Biology of Bees (Hymenoptera: Apoidea). St. Petersburg: Russian Academy of Sciences.
1996. "Protobee" and its nests: A new hypothesis concerning the early evolution of Apoidea (Hymenoptera). Entomol. Rev. 75: 140–162. [Translation of Radchenko and Pesenko, 1994a]
Rasnitsyn, A. P.
1975. Hymenoptera—Apocrita of the Mesozoic. Tr. Paleontol. Inst. Akad. Nauk SSSR 147: 1–132. [In Russian]
1988. An outline of evolution of the hymenopterous insects (order Vespida). Orient. Insects 22: 115–145.
Rasnitsyn, A. P., and C. D. Michener
1991. Miocene fossil bumble bee from the Soviet Far East with comments on the chronology and distribution of fossil bees (Hymenoptera: Apidae). Ann. Entomol. Soc. Am. 84: 583–589.
Rasnitsyn, A. P., E. A. Jarzembowski, and A. J. Ross
1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and pa-

laeoenvironmental significance. Cretac. Res. 19: 329–391.

Raven, P. H., and D. I. Axelrod
1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

Reyes, S. G.
1998. A cladistic analysis of the bee tribe Allodapini (Hymenoptera: Apidae: Xylocopinae). Philipp. Entomol. 12: 55–84.

Riou, B.
1999. Descriptions de quelques insectes fossiles du Miocène supérieur de la Montagne d'Andance. EPHE Biol. Evol. Insectes 11/ 12: 123–133.

Ritzkowski, S.
1997. K-Ar-Altersbestimmungen der bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). Metalla, Bochum 66: 19–23.

Robertson, C.
1903. Synopsis of Megachilidae and Bombinae. Trans. Am. Entomol. Soc. 29: 163–178.
1904. Synopsis of Anthophila. Can. Entomol. 36: 37–43.

Roig-Alsina, A., and C. D. Michener
1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). Univ. Kansas Sci. Bull. 55: 123–162.

Ronquist, F., A. P. Rasnitsyn, A. Roy, K. Eriksson, and M. Lindgren
1999. Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data. Zool. Scr. 28: 13–50.

Röschmann, F., and W. Mohrig
1995. Die Trauermücken des Sächsischen Bernsteins aus dem Untermiozän von Bitterfeld/Deutschland (Diptera, Sciaridae). Dtsch. Entomol. Z. 42: 17–54.

Roselli, F. L.
1938. Apuntes de geología y paleontología uruguaya. Sobre insectos del Cretácico del Uruguay o descubrimiento de admirables instintos constructivos de esa época. Bol. Soc. Amig. Cienc. Nat. "Kraglievich-Fontana" 1: 72–102.

Ross, A. J.
1998. Amber: The Natural Time Capsule. London: The Natural History Museum.

Ross, A. J., and P. V. York
2000. A list of type and figured specimens of insects and other inclusions in Burmese amber. Bull. Nat. Hist. Mus., London (Geol.) 56: 11–20.

Roubik, D. W.
1983. Nest and colony characteristics of stingless bees from Panamá. J. Kansas Entomol. Soc. 56: 327–355.

Roubik, D. W., J. E. Moreno, C. Vergara, and D. Wittmann
1986. Sporadic food competition with the African honey bee: Projected impact on neotropical social bees. J. Trop. Ecol. 2: 97–111.

Roussy, L.
1937. Contributions a l'etude de l'abeille Tertiaire, de ses parasites et de ses ennemis. Gaz. Apic., Montfavet 388: 49–72.
1960. Insectes et abeilles fossils de l'ambre de Sicile: Migrations, localisations, peuplement du Nouveau Monde, de l'Australie, de la Nouvelle Zelande. Gaz. Apic., Montfavet 635: 5–8.

Rozen, J. G., Jr.
1970. Biology, immature stages, and phylogenetic relationships of fideliine bees, with the description of a new species of *Neofidelia* (Hymenoptera, Apoidea). Am. Mus. Novitates 2427: 25 pp.
1973. Life history and immature stages of the bee *Neofidelia* (Hymenoptera, Fideliidae). Am. Mus. Novitates 2519: 14 pp.
1996. A new species of the bee Heterosarus from Dominican amber (Hymenoptera: Andrenidae; Panurginae). J. Kansas Entomol. Soc., Suppl. 69: 346–352. [Publ. date: 15 January 1997]
1997. South American rophitine bees (Hymenoptera: Halictidae: Rophitinae). Am. Mus. Novitates 3206: 27 pp.

Sakagami, S. F.
1959. Some interspecific relations between Japanese and European honeybees. J. Anim. Ecol. 28: 51–68.
1974. Sozialstruktur und Polymorphismus bei Furchen- und Schmalbienen. *In* G. H. Schmidt (ed.), Sozialpolymorphismus bei Insekten: 257–293. Stuttgart: Wissenschaftliche Verlagsgesellschaft MBH.
1976. Specific differences in the bionomic characters of bumblebees. A comparative review. J. Fac. Sci., Hokkaido Univ., ser. 6 (Zool.) 20: 390–447.
1978. *Tetragonula* stingless bees of the continental Asia and Sri Lanka (Hymenoptera, Apidae). J. Fac. Sci., Hokkaido Univ., ser. 6 (Zool.) 21: 165–247. [Publ. date: June 1978]

Sakagami, S. F., and C. D. Michener
1962. The Nest Architecture of the Sweat Bees (Halictinae): A Comparative

Study of Behavior. Lawrence KS: Univ. Kansas Press.

1987. Tribes of Xylocopinae and origin of the Apidae (Hymenoptera: Apoidea). Ann. Entomol. Soc. Am. 80: 439–450.

Salt, G.

1931. Three bees from Baltic amber. Bernstein-Forsch. 2: 136–147.

Sandhouse, G. A.

1943. The type species of the genera and subgenera of bees. Proc. U.S. Natl. Mus. 92: 519–619.

Saussure, H., de

1890. Histoire naturelle des Hyménoptères. *In* A. Grandidier (ed.), Histoire Physique, Naturelle et Politique de Madagascar, tome 20: 1–590. Paris: Imprimerie Nationale.

Schenck, A.

1860. Verzeichniss der nassauischen Hymenoptera aculeata. Stettiner Entomol. Ztg. 21: 132–157, 417–419.

1861. Die Nassauischen Bienen. Jahrb. Ver. Naturkd. Herzogthum Nassau 14: 1–414.

1869. Beschreibung der nassauischen Bienen, zweiter Nachtrag. Jahrb. Nassau. Ver. Naturkd. 21: 269–382. [Preprint, dated 1868, publ. 1869; refer to Michener (1986) for details of dating.]

Schultz, T. R., M. S. Engel, and M. Prentice

1999. Resolving conflict between morphological and molecular evidence for the origin of eusociality in the "corbiculate" bees (Hymenoptera: Apidae): A hypothesis-testing approach. Univ. Kansas Nat. Hist. Mus. Spec. Publ. 24: 125–138.

Schumann, H., and H. Wendt

1989. Kenntnis der tierischen Inklusen des Sächsischen Bernsteins. Dtsch. Entomol. Z. 36: 33–44.

Shedrinsky, A. M., D. Grimaldi, T. P. Wampler, and N. S. Baer

1991. Amber and copal: Pyrolysis gas chromatographic (PyGC) studies of provenance. Wiener Ber. Natwiss. Kunst 6–8: 37–63.

Shuckard, W. E.

1866. British Bees: An Introduction to the Study of the Natural History and Economy of the Bees Indigenous to the British Isles. London: Reeve and Co.

Silvestri, F.

1912. Die Thysanura des baltischen Bernsteins. Schr. Phys.-Ökon. Gesell. 53: 42–66.

Simmons, N. B., and J. H. Geisler

1998. Phylogenetic relationships of *Icaronycteris, Archaeonycteris, Hassianycteris,* and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bull. Am. Mus. Nat. Hist. 235: 182 pp.

Smith, F.

1853. Catalogue of Hymenopterous Insects in the Collection of the British Museum, Part 1: Andrenidae and Apidae. London: British Museum.

Snodgrass, R. E.

1935. Principles of Insect Morphology. New York: McGraw Hill.

1941. The male genitalia of Hymenoptera. Smithson. Misc. Coll. 99: 1–86.

1956. Anatomy of the Honey Bee. Ithaca NY: Cornell Univ. Press.

Spicer, R. A., P. McArees, and J. L. Chapman

1993. Cretaceous phytogeography and climate signals. Philos. Trans. R. Soc. London, ser. B, Biol. Sci. 341: 277–286.

Spinola, M.

1808. Insectorum Liguriae Species Novae aut Rariores, Quas in Agro Ligustico nuper Detexit, Descripsit, et Iconibus Illustravit Maximilianus Spinola, adjecto Catalogo Spiecierum Auctoribus jam Enumeratarum, Quae in Eadam Regione Occurrunt, vol. 2. Genuae: Gravier.

Statz, G.

1936. Ueber alte und neue fossile Hymenopterenfunde aus den tertiären Ablagerungen von Rott am Siebengebirge. Decheniana, Bonn 93: 256–312.

Stuckenberg, R. R.

1975. New fossil species of *Phlebotomus* and *Haematopota* in Baltic amber (Diptera: Psychodidae, Tabanidae). Ann. Natal Mus. 22: 455–464.

Sugden, E. A., R. W. Thorp, and S. L. Buchmann

1996. Honey bee-native bee competition in Australia: Focal point for environmental change and apicultural response. Bee World 77: 26–44.

Sun, G., D. L. Dilcher, S. Zheng, and Z. Zhou

1998. In search of the first flower: A Jurassic angiosperm, *Archaefructus,* from northeast China. Science 282: 1692–1695.

Taylor, D. W., and L. J. Hickey

1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Plant Syst. Evol. 180: 137–156.

Terzo, M.
1999. Révision du genre *Exoneuridia* Cockerell, 1911 (Hymenoptera Apoidea Xylocopinae Allodapini). Belg. J. Entomol. 1: 137–152.
Thomson, C. G.
1869. Opuscula Entomologica, Fasc. 1. Lund: Lundbergska.
Thorp, R. W.
1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann. Missouri Bot. Gard. 66: 788–812.
Tkalců, B.
1966. *Megabombus* (*Fervidobombus*) *abditus* sp. n. aus äquatorial-Afrika. Cas. Morav. Mus. Brne 51: 271–274.
Tosi, A.
1896. Di un nuovo genre di Apiaria fossile nell'ambra di Sicilia (*Meliponorytes succini—M. sicula*). Riv. Ital. Paleontol., Bologna 2: 352–356.
Turkin, N. I.
1997. Preliminary results of microscopic research of tangential wood imprints in Baltic amber. Metalla, Bochum 66: 55–56.
Unger, F.
1867. Die fossile Flora von Kumi auf der Insel Euboea. Denkschr. Kaiserl. Akad. Wiss., Math.-Natwiss. Cl. 27: 27–200.
Urban, D.
1967. As espécies do gênero *Thygater* Holmberg, 1884 (Hymenoptera, Apoidea). Bol. Univ. Fed. Paraná, Zool. II, 12: 177–309.
Weber, W. A.
1965. Theodore Dru Alison Cockerell, 1866–1948. Univ. Colorado Stud., Ser. Bibliogr. 1: 1–124.
2000. The American Cockerell: A Naturalist's Life, 1866–1948. Boulder: Univ. Press of Colorado.
Weitschat, W.
1997. Bitterfelder Bernstein—Ein eozäner Bernstein auf miozäner Lagerstätte. Metalla, Bochum 66: 71–84.
Weitschat, W., and W. Wichard
1998. Atlas der Pflanzen und Tiere im Baltischen Bernstein. München [Munich]: Verlag Friedrich Pfeil.
Wenner, A. M., and R. W. Thorp
1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. *In* W. L. Halverson and G. J. Maender (eds.), Fourth California Islands Symposium: Update on the Status of Resources: 351–365. Santa Barbara CA: Santa Barbara Mus. Nat. Hist.
Wheeler, W. M.
1914. The ants of the Baltic amber. Schr. Phys.-Ökon. Gesell. 55: 1–142.
Wilford, J. N.
1995. Which came first: bees or flowers? Find points to bees. New York Times, May 23: C1, C11.
Wille, A.
1959. A new stingless bee (Meliponini) from the amber of Chiapas, Mexico. J. Paleontol. 33: 849–852.
1977. A general review of the fossil stingless bees. Rev. Biol. Trop. 25: 43–46.
Wille, A., and L. C. Chandler
1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera; Meliponini). Rev. Biol. Trop. 12: 187–195.
Williams, P. H.
1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). Bull. Br. Mus. Nat. Hist. (Entomol.) 67: 79–152.
Winston, M. L., and C. D. Michener
1977. Dual origin of highly social behavior among bees. Proc. Natl. Acad. Sci., U.S.A. 74: 1135–1137.
Zeuner, F. E.
1931. Die Insektenfauna des Böttinger Marmors. Fortschr. Geol. Palaeontol. 9: 247–406.
1938. Die Insektenfauna des Mainzer Hydrobienkalks. Palaeontol. Z. 20: 104–159.
Zeuner, F. E., and F. J. Manning
1976. A monograph on fossil bees (Hymenoptera: Apoidea). Bull. Br. Mus. Nat. Hist. (Geol.) 27: 149–268.
Zhang, J.-F.
1990. New fossil species of Apoidea (Insecta: Hymenoptera). Acta Zootaxon. Sinica 15: 83–91. [In Chinese, with English summary]
Zhang, J.-F., B. Sun, and X.-Y. Zhang
1994. Miocene Insects and Spiders from Shanwang, Shandong. Beijing: Science Press. [In Chinese, with English summary]

APPENDIX 1

Bees in Amber and Copal

The following list enumerates those valid species presently recognized as inclusions in both amber and copal (synonymous names are not listed). The list excludes incertae sedis taxa. All species known from amber are extinct while only one of those recognized from copal is considered an extinct species (*Liotrigona vetula*).

The two meliponine species listed as in Sicilian amber (Tosi, 1896) may actually be in East African copal and synonymous with Recent stingless bee species. Unfortunately, Tosi's specimens were destroyed by a bomb during World War II and their true identity will, therefore, forever remain a mystery. *Apis catanensis,* also from Sicilian "amber", is listed, As discussed by Engel (1999c), *A. catanensis* is a *nomen dubium* and was perhaps not a bee at all (as suspected by Kohring and Schlüter, 1989); or, it may have been a living bee (*A. mellifera*) in African copal. Owing to the uncertainty over their identities, I have retained all of the Sicilian specimens in the list as bees occurring in true amber.

The Eocene amber of Arkansas is rich in insert inclusions. It will be interesting to see if bees are ever discovered from these deposits. Owing to the relative contemporaneous age with the Baltic amber fauna, the possibility of discovering similar taxa is tantalizing.

An annotated, general catalog of the world's species of fossil bees (both amber inclusions and compression fossils) as well as trace fossils attributed to bees will be presented elsewhere (Engel, in prep.)

Taxa	Deposit	Reference
AMBER BEES		
Apis catanensis [a]	Sicilian	Roussy, 1960; Engel, 1999c
Augochlora leptoloba	Dominican	Engel, 2000a
Boreallodape baltica	Baltic	this study
Boreallodape mollyae	Baltic	this study
Boreallodape striebichi	Baltic	this study
Chilicola electrodominica	Dominican	Engel, 1999f
Chilicola gracilis	Dominican	Michener and Poinar, 1996
Cretotrigona prisca	New Jersey	Michener and Grimaldi, 1988a; Engel, 2000b
Ctenoplectrella cockerelli	Baltic	this study
Ctenoplectrella grimaldii	Baltic	this study
Ctenoplectrella viridiceps	Baltic	Cockerell, 1909a; this study
Electrapis krishnorum	Baltic	this study
Electrapis martialis	Baltic	Cockerell, 1908b
Electrapis meliponoides	Baltic	Buttel-Reepen, 1906
Electrapis tornquisti	Baltic	Cockerell, 1909c
Electrobombus samlandensis	Baltic	this study
Electrolictus antiquus	Baltic	this study
Eomacropis glaesaria	Baltic	this study
Eufriesea melissiflora	Dominican	Poinar, 1998; Engel, 1999b
Euglossa moronei	Dominican	Engel, 1999b
Glaesosmia genalis	Baltic	this study
Glyptapis disareolata	Baltic	this study
Glyptapis densopunctata	Baltic	this study
Glyptapis fuscula	Baltic	Cockerell, 1909b; this study
Glyptapis mirabilis	Baltic	Cockerell, 1909a; this study
Heterosarus eickworti	Dominican	Rozen, 1996
Kelneriapis eocenica	Baltic	Kelner-Pillault, 1969a; this study
Liotrigonopsis rozeni	Baltic	this study
Megachile glaesaria	Dominican	Engel, 1999d
Melikertes clypeatus	Baltic	this study
Melikertes proavus	Baltic	Menge, 1856; this study
Melikertes stilbonotus	Baltic	Engel, 1998a; this study
Meliponorytes sicula	Sicilian	Tosi, 1896
Meliponorytes succini	Sicilian	Tosi, 1896
Melissites trigona	Baltic	this study
Neocorynura electra	Dominican	Engel, 1995

APPENDIX 1—(*Continued*)

Taxa	Deposit	Reference
Nogueirapis silacea	Mexican	Wille, 1959
Oligochlora eickworti	Dominican	Engel, 1996
Oligochlora grimaldii	Dominican	Engel, 1997
Oligochlora marquettorum	Dominican	Engel and Rightmyer, 2000
Oligochlora micheneri	Dominican	Engel, 1996
Oligochlora rozeni	Dominican	Engel, 2000a
Paleomelitta nigripennis	Baltic	this study
Proplebeia dominicana	Dominican	Wille and Chandler, 1964; Michener, 1982
Proplebeia tantilla	Dominican	Camargo et al., 2000
Proplebeia vetusta	Dominican	Camargo et al., 2000
Protobombus basilaris	Baltic	this study
Protobombus fatalis	Baltic	Cockerell, 1908b; this study
Protobombus indecisus	Baltic	Cockerell, 1908b; this study
Protobombus hirsutus	Baltic	Cockerell, 1908b; this study
Protobombus tristellus	Baltic	Cockerell, 1909c; this study
Protolithurgus ditomeus	Baltic	this study
Roussyana palmnickenensis	Baltic	Roussy, 1937; this study
Succinapis goeleti	Baltic	this study
Succinapis micheneri	Baltic	this study
Succinapis proboscidea	Baltic	this study
Thaumastobombus andreniformis	Baltic	this study
COPAL BEES (all extant except for *Liotrigona vetula*)		
Apis mellifera	East African	Foord, 1890; Cockerell, 1909a; Engel, personal obs.
Euglossa sp.[b]	Colombian	Engel, personal obs.; Ross, 1998
Heriades sp.[c]	East African	Engel, personal obs.
Hypotrigona gribodoi[d]	East African	Engel, personal obs.
Liotrigona vetula	African	Moure and Camargo, 1978
Meliponula erythra	East African	Zeuner and Manning, 1976; Wille, 1977
Trigona iridipennis[e]	Myanmar	Cockerell, 1921
Trigona lurida[f]	Colombian	Engel, personal obs.
Trigonisca sp.[f]	Colombian	Engel, personal obs.

[a] This species was considered a *nomen dubium* by Engel (1999c) and very likely not a bee. Kohring and Schlüter (1989) indicate it might have been a termite.

[b] Specimen in the Department of Palaeontology, Natural History Museum (British Museum), London.

[c] Specimen in the University Museum, Oxford.

[d] Specimens examined from various collections including the University Museum, Oxford; American Museum of Natural History, New York; and the Natural History Museum, London.

[e] Originally this specimen was proposed as an extinct species (*Meliponorytes devictus*) by Cockerell (1921) but has since been recognized as a subjective junior synonym of *T. iridipennis*, a widespread modern species (Kerr and Maule, 1964; Kerr and da Cunha, 1976; Zeuner and Manning, 1976; Wille, 1977). The resin in which the specimen resides was believed by Cockerell to be amber but it is actually copal (Ross and York, 2000).

[f] Specimens in the Central Texas Melittological Institute, Austin, Texas. I am grateful to John L. Neff for a loan of this material.

APPENDIX 2

Tribal Classification and Geological Distribution of Bees

The following outline presents the tribal classification of bees adopted by the present author based on continuing cladistic investigations into the higher-level phylogeny of Apoidea (figs. 122, 123). Some of these analyses have been presented above while others will be detailed in forthcoming papers. Those groups presently recorded from the geological record are followed by the standard geological abbreviation for their *oldest* epoch/stage [e.g., although numerous Miocene to Eocene fossils exist for Meliponini only Cretaceous/Maastrichtian (K/Maa) is listed owing to a single, older fossil from this period]. Compression fossils are indicated in boldface by **CF**, amber inclusions by **A**. Daggers (†) denote higher groups that are extinct.

Classification	Oldest Geological Record
FAMILY COLLETIDAE LEPELETIER DE SAINT FARGEAU	
Subfamily Colletinae Lepeletier de Saint Fargeau[a]	
Tribe Colletini Lepeletier de Saint Fargeau	
Tribe Paracolletini Cockerell	
Subfamily Stenotritinae Cockerell	
Subfamily Diphaglossinae Vachal	
Tribe Caupolicanini Michener	
Tribe Diphaglossini Vachal	
Tribe Dissoglottini Moure	
Subfamily Euryglossinae Michener	
Subfamily Hylaeinae Viereck	
Subfamily Xeromelissinae Cockerell	[Mio/Bur-Aqt (**A**)]
FAMILY HALICTIDAE THOMSON	
Subfamily Rophitinae Schenck	
Tribe Rophintini Schenck	
Tribe Penapini Engel	
Subfamily Nomiinae Robertson	
Subfamily Halictinae Thomson	
Tribe Nomioidini Börner	
Tribe Halictini Thomson	
Subtribe Halictina Thomson	[Eoc/Lut (**A**)]
Subtribe Sphecodina Schenck	
Tribe Gastrohalictini Schrottky	
Tribe Agapostemonini Engel	
Tribe Caenohalictini Michener	[Mio/Bur-Aqt (**A**)]
Tribe Augochlorini Beebe	
Subtribe Corynurina Engel	
Subtribe Augochlorina Beebe	[Mio/Bur-Aqt (**A**)]
FAMILY ANDRENIDAE LATREILLE	
Subfamily Andreninae Latreille	[Oli-Eoc/Rup-Prb (**CF**)]
Subfamily Alocandreninae Michener	
Subfamily Euherbstiinae Moure	
Subfamily Oxaeiinae Ashmead	
Subfamily Panurginae Leach	
Tribe Protandrenini Robertson[a]	[Mio/Bur-Aqt (**A**)]
Tribe Panurgini Leach[b]	
Tribe Melitturgini Newman[c]	
Tribe Meliturgulini Engel[d]	
Tribe Perditini Robertson	
Tribe Protomeliturgini Ruz	
Tribe Calliopsini Robertson	
†FAMILY PALEOMELITTIDAE ENGEL	[Eoc/Lut (**A**)]
FAMILY MELITTIDAE SCHENCK	
Subfamily Macropidinae Robertson	
†Tribe Eomacropidini Engel	[Eoc/Lut (**A**)]
Tribe Macropidini Robertson	

APPENDIX 2—(*Continued*)

Classification	Oldest Geological Record
FAMILY MELITTIDAE SCHENCK (*Continued*)	
Subfamily Melittinae Schenck	
Tribe Melittini Schenck	[Oli-Eoc/Rup-Prb (**CF**)]
Tribe Redivivini Engel	
Subfamily Dasypodainae Börner	
Tribe Promelittini Michener	
Tribe Dasypodaini Börner	[Mio/Lan (**CF**)]
Tribe Sambini Michener	
Subfamily Meganomiinae Michener	
FAMILY MEGACHILIDAE LATREILLE	
Subfamily Fideliinae Cockerell	
Tribe Fideliini Cockerell	
Tribe Pararhophitini Popov	
Subfamily Lithurginae Newman	
†Tribe Protolithurgini Engel	[Eoc/Lut (**A**)]
Tribe Lithurgini Newman	[Mio/Aqt (**CF**)]
Subfamily Megachilinae Latreille	
Tribe Osmiini Newman[e]	
†Subtribe Ctenoplectrellina Engel	[Eoc/Lut (**A**)]
†Subtribe Glyptapina Cockerell	[Eoc/Lut (**A**)]
Subtribe Trypetina Robertson	[Oli-Eoc/Rup-Prb (**CF**)]
Subtribe Osmiina Newman	[Oli/Rup (**CF**)]
Tribe Anthidiini Ashmead	
Subtribe Anthidiina Ashmead	[Oli-Eoc/Rup-Prb (**CF**)]
Subtribe Dioxyina Cockerell	
Tribe Megachilini Latreille	[Oli-Eoc/Rup-Prb (**CF**)]
FAMILY APIDAE LATREILLE	
Subfamily Xylocopinae Latreille	
Tribe Xylocopini Latreille	[Oli-Eoc/Rup-Prb (**CF**)]
Tribe Manueliini Sakagami and Michener	
Tribe Ceratinini Latreille	[Oli-Eoc/Rup-Prb (**CF**)]
†Tribe Boreallodapini Engel	[Eoc/Lut (**A**)]
Tribe Allodapini Cockerell	
Subfamily Nomadinae Latreille	
Tribe Hexepeolini Roig-Alsina and Michener	
Tribe Brachynomadini Roig-Alsina and Michener	
Tribe Townsendiellini Michener	
Tribe Biastini Linsley and Michener	
Tribe Nomadini Latreille	
Tribe Epeolini Robertson	
Tribe Ammobatoidini Michener	
Tribe Neolarrini Fox	
Tribe Ammobatini Handlirsch	
Tribe Caenoprosopidini Michener	
Subfamily Apinae Latreille	
The Euceriti Line	
Tribe Osirini Handlirsch	
Tribe Isepeolini Rozen, Eickwort, and Eickwort	
Tribe Protepeolini Linsley and Michener	
Tribe Exomalopsini Vachal	
Tribe Ancylini Michener	

APPENDIX 2—(*Continued*)

Classification	Oldest Geological Record
Subfamily Apinae Latreille *(continued)*	
The Euceriti Line (continued)	
Tribe Teratognathini Silveira	
Tribe Eucerini Latreille	[Oli/Rup (**CF**)]
Tribe Ctenoplectrini Cockerell	
Tribe Emphorini Robertson	
Tribe Tapinotaspidini Roig-Alsina and Michener	
The Apiti Line	
Tribe Tetrapediini Michener and Moure	
Tribe Rhathymini Lepeletier de Saint Fargeau	
Tribe Ericrocidini Cockerell and Atkins	
Tribe Melectini Westwood	[Oli-Eoc/Rup-Prb (**CF**)]
Tribe Anthophorini Dahlbom	[Oli-Eoc/Rup-Prb (**CF**)]
Tribe Centridini Cockerell and Cockerell	
"Corbiculate Apinae"	
Tribe Euglossini Latreille	[Mio/Bur-Aqt (**A**)]
Tribe Bombini Latreille	[Oli-Eoc/Rup-Prb (**CF**)]
†Tribe Electrobombini Engel	[Eoc/Lut (**A**)]
†Tribe Electrapini Engel	[Eoc/Lut (**A**)]
Tribe Meliponini Lepeletier de Saint Fargeau	[K/Maa (**A**)]
†Tribe Melikertini Engel	[Eoc/Lut (**A**)]
Tribe Apini Latreille	[Oli/Cht-Rup (**CF**)]

[a]This group is demonstrably paraphyletic and will require splitting.

[b]The tribes Camptopoeumini and Panurginini of Patiny (1999) are newly synonymized here.

[c]The tribe Mermiglossini of Patiny (1999) is newly synonymized here.

[d]New tribe (type genus: *Meliturgula* Friese); proposed to replace the tribe Paramelitturgini of Patiny (1999). Paramelitturgini is unavailable since it was not based on an available genus-group name (ICZN, 1999b: Art. 11.7.1.1). The composition and diagnosis of the tribe is presented by Patiny (1999: 272).

[e]The subtribes included here will eventually need to be elevated to tribal rank (along with other generic groups of Osmiini) since the tribe is presently paraphyletic.

APPENDIX 3

Catalog of Family- and Genus-Group Names for Fossil Bees

The following catalog presents all known family- and genus-group names proposed for fossil bees (amber inclusions and compression fossils). Not all of the names are currently recognized as valid (e.g., *Sophrobombus* is a synonym of *Protobombus*; *Paleoeuglossa* is a synonym of *Eufriesea*) or are confidently assigned to higher categories (e.g., *Protomelecta*); thus this list should not be taken as a classification. At the end of the list I have included two genus-group names originally proposed as fossil bees but subsequently recognized to be insects other than bees. A catalog of the world's species of fossil bees (both amber inclusions and compression fossils) will be presented elsewhere (Engel, in prep.).

The format is generally that of Michener (1986) for family-group names and Michener (1997) for genus-group names. For family-group names I have indicated the higher group to which a given taxon belongs. The number that indicates the location of the name in the system of Michener (1986: with additions and corrections by Michener, 1997) is appended at the end of each entry.

The citation "Engel (2001)" in the following list refers to the present monograph and those names newly proposed in the body of the text; thus, this reference will not be found in the bibliography.

Family-Group Names (10 names)

Boreallodapini Engel, 2001: 77. Type genus: *Boreallodape* Engel, 2001. Stem: Boreallodap-. **Apidae: Xylocopinae** [M86/97–120.2].

Chalicodomopsini Engel, 1999d: 4. Type genus: *Chalicodomopsis* Engel, 1999d. Stem: Chalicodomops-. **Megachilidae: Megachilinae** [M86/97–67.2]. *Nomen nudum.*

Ctenoplectrellina Engel, 2001: 54. Type genus: *Ctenoplectrella* Cockerell, 1909a. Stem: Ctenoplectrell-. **Megachilidae: Megachilinae** [M86/97–67.3].

Electrapina Engel, 1998a: 99. Type genus: *Electrapis* Cockerell, 1908b. Stem: Electrap-. **Apidae: Apinae** [M86/97–129.1].

Electrobombini Engel, 2001: 88. Type genus: *Electrobombus* Engel, 2001. Stem: Electrobomb-. **Apidae: Apinae** [M86/97–129.2].

Eomacropidini Engel, 2001: 46. Type genus: *Eomacropis* Engel, 2001. Stem: Eomacropid-. **Melittidae: Macropidinae** [M86/97–57.2].

Glyptapinae Cockerell, 1909b: 13. Type genus: *Glyptapis* Cockerell, 1909a. Stem: Glyptap-. **Megachilidae: Megachilinae** [M86/97–67.1].

Melikertini Engel, 2001: 112. Type genus: *Melikertes* Engel, 1998a. Stem: Melikert-. **Apidae: Apinae** [M86/97–129.3].

Paleomelittidae Engel, 2001: 41. Type genus: *Paleomelitta* Engel, 2001. Stem: Paleomelitt-. **Paleomelittidae** [M86/97–57.1].

Protolithurgini Engel, 2001: 51. Type genus: *Protolithurgus* Engel, 2001. Stem: Protolithug-. **Megachilidae: Lithurginae** [M86/97–61.1].

Genus-Group Names (47 names)

Anthophorites Heer, 1849: 97. Type species: *Anthophorites mellona* Heer, 1849, by designation of Cockerell, 1909a. **Apidae: Anthophorini?.**

Apiaria Germar, 1839: 210. Type species: *Apiaria dubia* Germar, 1839, monobasic. **Megachilidae: Osmiini?.**

Bombusoides Motschulsky, 1856: 28. Type species: *Bombusoides mengei* Motschulsky, 1856, monobasic. **Incertae sedis.**

Boreallodape Engel, 2001: 78. Type species: *Boreallodape baltica* Engel, 2001, original designation. **Xylocopinae: Boreallodapini.**

Calyptapis Cockerell, 1906: 41. Type species: *Calyptapis florissantensis* Cockerell, 1906, monobasic. **Apidae: Bombini.**

Cascapis Engel, 1999c: 187. Type species: *Apis armbrusteri* Zeuner, 1931, monobasic and original designation, isotypic with *Hauffapis.* Proposed as a subgenus of *Apis.***Apidae: Apini.**

Chalcobombus Cockerell, 1908b: 326. Type species: *Chalcobombus humilis* Cockerell, 1908b [= *Protobombus indecisus* Cockerell, 1908b], by designation of Cockerell, 1909b; isotypic with *Protobombus* Cockerell, 1908b, by synonymy. **Apidae: Apinae: Electrapini.**

Chalicodomopsis Engel, 1999d: 3. Type species: *Megachile* (*Chalicodomopsis*) *glaesaria* Engel, 1999d, monobasic and original designation. Proposed as a subgenus of *Megachile.* **Megachilidae: Megachilini.**

Cretotrigona Engel, 2000b: 3. Type species: *Trigona* (*Trigona*) *prisca* Michener and Grimaldi, 1988a, monobasic and original designation. **Apidae: Meliponini.**

Ctenoplectrella Cockerell, 1909a: 314. Type species: *Ctenoplectrella viridiceps* Cockerell, 1909a, monobasic. **Megachilidae: Megachilinae: Osmiini.**

Cyrtapis Cockerell, 1908a: 339. Type species: *Cyrtapis anomalus* Cockerell, 1908a, monobasic. **Halictidae: Halictini.**

Eckfeldapis Lutz, 1993: 180. Type species:

Eckfeldapis electrapoides Lutz, 1993, monobasic and original designation. **Apidae: Apinae: Electrapini.**

Eickwortapis Michener and Poinar, 1996 [1997]: 354. Type species: *Eickwortapis dominicana* Michener and Poinar, 1996, monobasic and original designation. **Halictidae: Caenohalictini.**

Electrapis Cockerell, 1908b: 326. Type species: *Apis meliponoides* Buttel-Reepen, 1906, by designation of Cockerell, 1909b. **Apidae: Apinae: Electrapini.**

Electraugochlora Engel, 2000a: 32. Type species: *Augochlora* (*Electraugochlora*) *leptoloba* Engel, 2000a. Proposed as a subgenus of *Augochlora.* **Halictidae: Augochlorini.**

Electrobombus Engel, 2001: 88. Type species: *Electrobombus samlandensis* Engel, 2001, monobasic and original designation. **Apidae: Apinae: Electrobombini.**

Electrolictus Engel, 2001: 38. Type species: *Electrolictus antiquus* Engel, 2001, monobasic and original designation. **Halictidae: Halictini.**

Eomacropis Engel, 2001: 46. Type species: *Eomacropis glaesaria* Engel, 2001, monobasic and original designation. **Melittidae: Macropidinae: Eomacropidini.**

Glaesosmia Engel, 2001: 75. Type species: *Glaesosmia genalis* Engel, 2001, monobasic and original designation. **Megachilidae: Megachilinae: Osmiini.**

Glyptapis Cockerell, 1909a: 314. Type species: *Glyptapis mirabilis* Cockerell, 1909a, monobasic. **Megachilidae: Megachilinae: Osmiini.**

Hauffapis Armbruster, 1938: 37. Type species: *Hauffapis scheuthlei* Armbruster, 1938 [=*Apis armbrusteri* Zeuner, 1931], by designation of Zeuner and Manning, 1976, isotypic with *Cascapis.* Unavailable as no type species was originally designated (required after 1930 by ICZN, 1999b: Art. 13.3). Note: Zeuner and Manning's action does not validate the name with themselves as authors as it was in the synonymy of the genus. **Apidae: Apini.**

Kelneriapis Sakagami, 1978 (June): 232. Type species: *Hypotrigona eocenica* Kelner- Pillault, 1969a, monobasic, isotypic with *Kelnermelia.* Proposed as a subgenus of *Tetragonula.* **Apidae: Meliponini.**

Kelnermelia Moure *In* Moure and Camargo, 1978 (November): 565. Type species: *Hypotrigona eocenica* Kelner-Pillault, 1969a, monobasic and original designation, isotypic with *Kelneriapis.* **Apidae: Meliponini.**

Libellulapis Cockerell, 1906: 42. Type species: *Libellulapis antiquorum* Cockerell, 1906, monobasic. **Andrenidae: Panurginae?.**

Liotrigonopsis Engel, 2001: 135. Type species: *Liotrigonopsis rozeni* Engel, 2001, monobasic and original designation. **Apidae: Meliponini.**

Lithandrena Cockerell, 1906: 44. Type species: *Lithandrena saxorum* Cockerell, 1906, monobasic. **Andrenidae: Andreninae?.**

Lithanthidium Cockerell, 1911b: 225. Type species: *Lithanthidium pertriste* Cockerell, 1911b, monobasic. **Megachilidae: Anthidiini.**

Melikertes Engel, 1998a: 95. Type species: *Electrapis* (*Melikertes*) *stilbonota* Engel, 1998a, original designation. Proposed as a subgenus of *Electrapis.* **Apidae: Apinae: Melikertini.**

Meliponorytes Tosi, 1896: 352. Type species: *Meliponorytes succini* Tosi, 1896, by designation of Sandhouse, 1943. **Apidae: Meliponini.**

Melissites Engel, 2001: 129. Type species: *Melissites trigona* Engel, 2001, monobasic and original designation. **Apidae: Apinae: Melikertini.**

Oligochlora Engel, 1996 [1997]: 336. Type species: *Oligochlora eickworti* Engel, 1996, original designation. **Halictidae: Augochlorini.**

Paleoeuglossa Poinar, 1998 [1999]: 30. Type species: *Paleoeuglossa melissiflora* Poinar, 1998, monobasic and original designation. **Apidae: Euglossini.**

Paleomelitta Engel, 2001: 42. Type species: *Paleomelitta nigripennis* Engel, 2001, monobasic and original designation. **Paleomelittidae.**

Pelandrena Cockerell, 1909d: 159. Type species: *Pelandrena reducta* Cockerell, 1909d, monobasic. **Andrenidae: Andreninae?.**

Priorapis Engel, 1999c: 188. Type species: *Apis vetusta* Engel, 1998c, monobasic and original designation. Proposed as a subgenus of *Apis.* **Apidae: Apini.**

Probombus Piton, 1940: 218. Type species: *Probombus hirsutus* Piton, 1940, monobasic. **Apidae: Bombini.**

Prohalictus Armbruster, 1938: 48. Type species: *Prohalictus schemppi* Armbruster, 1938, monobasic. **Halictidae: Halictini.**

Proplebeia Michener, 1982: 44. Type species: *Trigona* (*Liotrigona*) *dominicana* Wille and Chandler, 1964, monobasic and original designation. Proposed as a subgenus of *Trigona.* **Apidae: Meliponini.**

Protobombus Cockerell, 1908b: 326. Type species: *Protobombus indecisus* Cockerell, 1908b, monobasic [also designated by Cockerell, 1909b], isotypic with *Chalcobombus* Cockerell, 1908b, by synonymy. **Apidae: Apinae: Electrapini.**

Protolithurgus Engel, 2001: 51. Type species: *Protolithurgus ditomeus* Engel, 2001, monobasic and original designation. **Megachilidae: Lithurginae: Protolithurgini.**

Protomelecta Cockerell, 1908a: 341. Type species: *Protomelecta brevipennis* Cockerell, 1908a, monobasic. **Apidae: Melectini?.**

Roussyana Manning, 1960 [1961]: 306. Type species: *Apis palmnickenensis* Roussy, 1937, original designation. Proposed as a subgenus of *Electrapis.* **Apidae: Apinae: Melikertini.**

Soliapis Engel, 2000a: 47. Type species: *Oligochlora* (*Soliapis*) *rozeni* Engel, 2000a, original designation. Proposed as a subgenus of *Oligochlora.* **Halictidae: Augochlorini.**

Sophrobombus Cockerell, 1908b: 326. Type species: *Sophrobombus fatalis* Cockerell, 1908b, monobasic [also designated by Cockerell, 1909c]. **Apidae: Apinae: Electrapini.**

Succinapis Engel, 2001: 115. Type species: *Succinapis goeleti* Engel, 2001, original designation. **Apidae: Apinae: Melikertini.**

Synapis Cockerell, 1907: 229. Type species: *Apis* (*Synapis*) *henshawi* Cockerell, 1907, monobasic. Proposed as a subgenus of *Apis.* **Apidae: Apini.**

Thaumastobombus Engel, 2001: 109. Type species: *Thaumastobombus andreniformis* Engel, 2001, monobasic and original designation. **Apidae: Apinae: Electrapini.**

Non-Bees

Palaeapis Hong, 1984: 37. Type species: *Palaeapis beiboziensis* Hong, 1984, monobasic and original designation. Originally proposed in Apidae; presently a junior synonym of *Archisphex* (Rasnitsyn et al., 1998). **Sphecidae.**

Sinostigma Hong, 1983: 9. Type species: *Sinostigma spinalata* Hong, 1983, monobasic and original designation. Originally proposed in Melittidae; later transferred to Megachilidae (Hong, 1985). **Vespidae?.**

APPENDIX 4

Full Journal Titles Abbreviated in References

The following list provides full journal titles for abbreviations in the References section. Abbreviations are listed in alphabetical order in boldface, followed by the expanded title. Specific series or report numbers are replaced in this list by "#".

Acta Zootaxon. Sinica Acta Zootaxonomica Sinica

Am. Chem. Soc. American Chemical Society

Am. J. Bot. American Journal of Botany

Am. Midl. Nat. American Midland Naturalist

Am. Mus. Novitates American Museum Novitates

Ann. Entomol. Soc. Am. Annals of the Entomological Society of America

Ann. Geol. Pays Helleniques Annales Geologiques des Pays Helleniques

Ann. Mag. Nat. Hist., ser. # Annals and Magazine of Natural History, series #

Ann. Missouri Bot. Gard. Annals of the Missouri Botanical Garden

Ann. Natal Mus. Annals of the Natal Museum

Ann. Soc. Entomol. Fr. Annales de la Société Entomologique de France

Annu. Rev. Ecol. Syst. Annual Review of Ecology and Systematics

Annu. Rev. Entomol. Annual Review of Entomology

Appl. Spectrosc. Rev. Applied Spectroscopy Reviews

Arch. Bienenkd. Archiv für Bienenkunde

Arq. Mus. Parana. Arquivos do Museu Paranaense

Aust. J. Sci. Australian Journal of Science

Aust. Zool. Australian Zoologist

Belg. J. Entomol. Belgian Journal of Entomology

Bernstein-Forsch. Bernstein-Forschungen

Biol. J. Linn. Soc. Biological Journal of the Linnean Society

Biol. Zentbl. Biologisches Zentralblatt

Biul. Inst. Geol. Biuletyn Instytutu Geologicznego

Bol. Soc. Amig. Cienc. Nat. "Kraglievich-Fontana" Boletín de la Sociedad Amigos de las Ciencias Naturales "Kraglievich-Fontana"

Bol. Univ. Fed. Paraná, Zool. # Boletim da Universidade Federal do Paraná, Zoologia

Bot. Gaz. Botanical Gazette

Bull. Am. Mus. Nat. Hist. Bulletin of the American Museum of Natural History

Bull. Br. Mus. Nat. Hist. (Entomol.) Bulletin of the British Museum of Natural History (Entomology)

Bull. Br. Mus. Nat. Hist. (Geol.) Bulletin of the British Museum of Natural History (Geology)

Bull. Mus. Comp. Zool. Bulletin of the Museum of Comparative Zoology

Bull. Nat. Hist. Mus., London (Geol.) Bulletin of the Natural History Museum, London (Geology)

Bull. Pol. Acad. Sci. Bulletin of the Polish Academy of Sciences

Bull. Soc. Entomol. France Bulletin de la Société Entomologique de France

Bull. Tianjin Inst. Geol. Miner. Res. Bulletin of the Tianjin Institute of Geology and Mineral Resources

Bull. Zool. Nomencl. The Bulletin of Zoological Nomenclature
Can. Entomol. The Canadian Entomologist
Cas. Morav. Mus. Brne Časopis Moravského musea v Brne
Chácaras Quint. (São Paulo) Chácaras e Quintais, São Paulo
Contrib. Am. Entomol. Inst. Contributions of the American Entomological Institute
Contrib. Geol., Univ. Wyoming. Contributions to Geology, University of Wyoming
Cretac. Res. Cretaceous Research
Dalle Mem. Soc. Entomol. Ital. Dalle Memorie della Societa Entomologica Italiana
Denkschr. Kaiserl. Akad. Wiss., Math.-Natwiss. Cl. Denkschriften der Kaiserlichen Akademie der Wissenschaften [Wien], Mathematisch-Naturwissenschaftliche Classe
Doc. Nat. Documenta Naturae
Dtsch. Entomol. Z. Detusche Entomologische Zeitschrift
Entomol. Entomologist
Entomol. Mag. Entomological Magazine
Entomol. News Entomological News
Entomol. Obozr. Entomologicheskoye Obozreniye
Entomol. Rev. Entomological Review
Entomol. Scand. Entomologica Scandinavica
EPHE Biol. Evol. Insectes EPHE Biologie et Evolution des Insectes
Etude Entomol. Etude Entomologiques
Fortschr. Geol. Palaeontol. Fortschritte der Geologie und Palaeontologie
Gaz. Apic., Montfavet La Gazette Apicole, Montfavet
J. Anim. Ecol. Journal of Animal Ecology
J. Baltic Stud. Journal of Baltic Studies
J. Evol. Biol. Journal of Evolutionary Biology
J. Exp. Biol. Journal of Experimental Biology
J. Fac. Sci., Hokkaido Univ., ser. # (Zool.) Journal of the Faculty of Science, Hokkaido University, series # (Zoology)
J. Hym. Res. Journal of Hymenoptera Research
J. Kansas Entomol. Soc. Journal of the Kansas Entomological Society
J. Kansas Entomol. Soc., Suppl. Journal of the Kansas Entomological Society, Supplement
J. New York Entomol. Soc. Journal of the New York Entomological Society
J. Paleontol. Journal of Paleontology
J. Trop. Ecol. Journal of Tropical Ecology
Jahrb. Nassau. Ver. Naturkd. Jahrbücher des Nassauischen Vereins für Naturkunde
Jahrb. Ver. Naturkd. Herzogthum Nassau Jahrbücher des Vereins für Naturkunde im Herzogthum Nassau
Linzer Biol. Beitr. Linzer Biologische Beiträge
Lunds Univ. Årskr., 2 Afd. Lunds Universitets Årsskrift, 2 Afdelning, Medicin samt Matematiska och Naturvetenskapliga Ämnen [Parallel serial title: Acta Universitatis Lundensis]
Mag. Insektenkd. Magazin für Insektenkunde
Mainzer Natwiss. Arch. Mainzer naturwissenschaftliches Archiv
Mem. Beijing Nat. Hist. Mus. Memoirs of the Beijing Natural History Museum
Mitt. Geol.-Paläontol. Inst. Univ. Hambg. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg
Mitt. Zool. Mus. Berl. Mitteilungen aus dem Zoologischen Museum in Berlin
Mol. Phylogenet. Evol. Molecular Phylogenetics and Evolution
Münster. Forsch. Geol. Paläontol. Münstersche Forschungen zur Geologie und Paläontologie
Mus. North. Arizona Bull. Museum of Northern Arizona Bulletin
Natl. Park Serv., Paleontol. Res. [Tech. Rep. #] National Park Service, Paleontological Research [Technical Report]
Neue Denkschr. Allg. Schweiz. Gesell. Ges. Natwiss. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften
Nova Acta Acad. C. Leopold.-Carol. Germ. Nat. Cur. Nova Acta Academiae Caesarea Leopoldino-Carolinae Germanicum Naturae Curiosorum
Nova Acta Leopold. (Kaiserl. Leopold.-Carol. Dtsch. Akad. Naturf.) Nova Acta Leopoldina (Kaiserlich Leopoldinisch-Carolinisch Deutschen Akademie der Naturforscher)
Orient. Insects Oriental Insects
Palaeogeogr., Palaeoclimatol., Palaeoecol. Palaeogeography, Palaeoclimatology, Palaeoecology
Palaeontol. Z. Palaeontologische Zeitschrift
Pan-Pac. Entomol. Pan-Pacific Entomologist
Pap. Avulsos Zool. (São Paulo) Papéis avulsos de Zoologia, São Paulo
Philipp. Entomol. Philippine Entomologist
Philos. Trans. R. Soc. London, ser. B, Biol. Sci. Philosophical Transactions of the Royal Society of London, series B, Biological Sciences
Plant Syst. Evol.=Plant Systematics and Evolution
Plateau J., Mus. North. Arizona=Plateau Journal, Museum of Northern Arizona
Proc. Acad. Nat. Sci., Philadelphia Proceedings of the Academy of Natural Sciences, Philadelphia
Proc. Natl. Acad. Sci., U.S.A. Proceedings of the National Academy of Sciences of the United States of America

Proc. First Intl. Palaeoentomol. Conf., Moscow Proceedings of the First International Palaeoentomological Conference, Moscow [Russia]
Proc. VI Congr. IUSSI, Bern Proceedings VI Congress of the International Union for the Study of Social Insects, Bern [Switzerland]
Proc. 13th Intl. Congr. IUSSI, Adelaide- Proceedings of the 13th International Congress of the International Union for the Study of Social Insects, Adelaide [Australia]
Proc. U.S. Natl. Mus. Proceedings of the United States National Museum
Prof. Pap. Stratigr. Paleontol. Professional Papers of Stratigraphy and Paleontology
Rev. Biol. Trop. Revista de Biología Tropical
Rev. Palaeobot. Palynol. Review of Palaeobotany and Palynology
Rev. Zool. Bot. Afr. Revue de Zoologie et de Botanique Africaines
Riv. Ital. Paleontol., Bologna Rivista Italiana di Paleontologia, Bologna [Italy]
Rocky Mountain Sec., Geol. Soc. Am. Reg. Meeting Rocky Mountain Section, Geological Society of America Regional Meeting
Russian Acad. Sci. Russian Academy of Sciences
Schr. Naturf. Gesell. Danzig Schriften der Naturforschenden Gesellschaft in Danzig
Schr. Phys.-Ökon. Gesell. Schriften der Physikalisch-ökonomischen Gesellschaft
Sitzungsber. Akad. Wiss. Wien, Math.-Natwiss. Kl. Sitzungsberichte der Akademie der Wissenschaften in Wien [Vienna], Mathematische-Naturwissenschaftliche Klasse
Smithson. Misc. Coll. Smithsonian Miscellaneous Collections
Sociobiol. Sociobiology
Stettiner Entomol. Ztg. Stettiner Entomologische Zeitung
Stud. Entomol. Studia Entomologia
Stud. Geol. Salmanticensia (Stud. Palaeocheloniol.) Studia Geologica Salmanticensia (Studia Palaeochelonіological)
Syst. Entomol. Systematic Entomology
Syst. Zool. Systematic Zoology
Tr. Paleontol. Inst. Akad. Nauk SSSR Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR
Trans. Am. Entomol. Soc. Transactions of the American Entomological Society
Trans. Entomol. Soc. London Transactions of the Entomological Society of London
Trans. Norfolk Norwich Nat. Soc. Transactions of the Norfolk and Norwich Naturalist's Society
Univ. California Publ. Entomol. University of California Publications in Entomology
Univ. Colorado Stud., Ser. Bibliogr. University of Colorado Studies, Series in Bibliography
Univ. Kansas Nat. Hist. Mus. Sci. Pap. Scientific Papers, Natural History Museum, University of Kansas
Univ. Kansas Nat. Hist. Mus. Spec. Publ. University of Kansas Natural History Museum Special Publication
Univ. Kansas Sci. Bull. University of Kansas Science Bulletin
U.S. Geol. Surv. Bull., Washington United States Geological Survey Bulletin, Washington [D.C.]
Usp. Sovrem. Biol., Moscow Uspechi sovremennoi Biologii, Moscow
Verh. XI Intl. Kongr. Entomol., Wien Verhandlungen XI Internationaler Kongress für Entomologie, Wien [Vienna]
Verh. Naturhist. Ver. Preuss. Rheinlande Westphalen Verhandlungen des Naturhistorischen Vereines der Preussischen Rheinlande und Westphalen
Wiener Ber. Natwiss. Kunst Wiener berichte über Naturwissenschaft in der Kunst
Zool. Inst., Acad. Sci. Zoological Institute, Academy of Sciences
Zool. J. Linn. Soc. Zoological Journal of the Linnean Society
Zool. Scr. Zoologica Scripta
Z. Syst. Hym. Dipt. Zeitschrift für systematische Hymenopterologie und Dipterologie

INDEX OF TAXONOMIC NAMES

Page of original reference in Roman typeface; figures in italics. Specific names are cited individually, with current generic combination indicated in parentheses. Names in the family-group are in capitals.

Andrena, 138
andreniformis (*Thaumastobombus*), 109,*110–114,190*
antiquus (*Electrolictus*), *38,*39,*40,41,186*
APIDAE, 76
APIFORMES, 35
APINAE, 86
Apis, 94,98,124,131
APOIDEA, 34
apoides (*Protobombus*; *=indecisus*), 101
baltica (*Boreallodape*), 79,*78–80,189*
basilaris (*Protobombus*), 105,*106*
Bombus, 138
Bombusoides, 138
bombusoides (*Electrapis*; *=tornquisti*), 96
Boreallodape, 78
BOREALLODAPINI, 77
carbonarius ("*Bombus*"), 138
Chalcobombus (*=Protobombus*), 100
clypeatus (*Melikertes*), 128,*192*
cockerelli (*Ctenoplectrella*), 71,*72*
cockerelli (*Electrapis*; *=tornquisti*), 96
Ctenoplectrella, 68
CTENOPLECTRELLINA, 54
Dasypoda, 64
densopunctata (*Glyptapis*), 62,*63,188*
dentata (*Ctenoplectrella*; *=viridiceps*), 69
disareolata (*Glyptapis*), 59,*60–62,187*
ditomeus (*Protolithurgus*), 51,*52,187*
Eckfeldapis (*=Electrapis*), 92
ELECTRAPINI, 90
Electrapis, 92
ELECTROBOMBINI, 88
Electrobombus, 88
Electrolictus, 38
eocenica (*Kelneriapis*), *133,*134,*192*
EOMACROPIDINI, 46
Eomacropis, 46
fatalis (*Protobombus*), 103,*104*
fuscula (*Glyptapis*), *62,*64,*65,66,188*
genalis (*Glaesosmia*), 75,*75*
glaesaria (*Eomacropis*), 47,*47,48,186*
Glaesosmia, 75
GLYPTAPINA, 54
Glyptapis, 56
goeleti (*Succinapis*), 115,*116–118,192*
grimaldii (*Ctenoplectrella*), 73,*74,188*
HALICTIDAE, 36
HALICTINAE, 36
HALICTINI, 37
hermenaui (*Electrapis*; *=tornquisti*), 96
hirsutus (*Protobombus*), *106,*108,*190*
humilis (*Protobombus*; *=indecisus*), 101
Hypotrigona, 134
indecisus (*Protobombus*), *100,*101,*102,191*
Kelneriapis, 134
Kelnermelia (*=Kelneriapis*), 134
krishnorum (*Electrapis*), 94,*94,96*
Liotrigonopsis, 135
LITHURGINAE, 50
MACROPIDINAE, 46
martialis (*Electrapis*), *92,*93
Megachile, 75
MEGACHILIDAE, 49
MEGACHILINAE, 53
Melikertes, 123
MELIKERTINI, 112
MELIPONINI, 133
meliponoides (*Electrapis*), 98,*98,191*
Melissites, 129
MELITTIDAE, 44
MELITURGULINI, 177,179
mengei (*Bombusoides*), 139
micheneri (*Succinapis*), 118,*120,192*
minuta (*Roussyana*; *=palmnickenensis*), 132
mirabilis (*Glyptapis*), *2,55,*57,*58,187*
mollyae (*Boreallodape*), 81,*81,82,189,190*
muscorum ("*Bombus*"), 138
neglecta (*Glyptapis*; *=fuscula*), 64
nigripennis (*Paleomelitta*), 42,*42–44,186,187*
OSMIINA, 54
OSMIINI, 54
Paleomelitta, 42
PALEOMELITTIDAE, 41
palmnickenensis (*Roussyana*), 131
PENAPINI, 37
proavus (*Melikertes*), 124
proboscidea (*Succinapis*), 121,*122,192*
Protobombus, 99
PROTOLITHURGINI, 51
Protolithurgus, 51
pusillus ("*Bombus*"), 138
REDIVIVINI, 45
reducta (*Glyptapis*; *=fuscula*), 64
reticulata (*Glyptapis*; *=fuscula*), 64
Roussyana, 131
rozeni (*Liotrigonopsis*), 136,*136,137,192*
samlandensis (*Electrobombus*), 88,*89,90,190*
Sophrobombus (*=Protobombus*), 100
splendens (*Ctenoplectrella*; *=viridiceps*), 69
stilbonotus (*Melikertes*), 126,*125–127*
striebichi (*Boreallodape*), 82,*83–86,189*
Succinapis, 115
Tetragonula, 134
Thaumastobombus, 109
tornquisti (*Electrapis*), 96
Trigona, 124,132,134
trigona (*Melissites*), 129,*129–131,191*
tristellus (*Protobombus*), 107
TRYPETINA, 54
viridiceps (*Ctenoplectrella*), *68,*69,*70,188*
wrisleyi ("*Andrena*"), 138
XYLOCOPINAE, 77

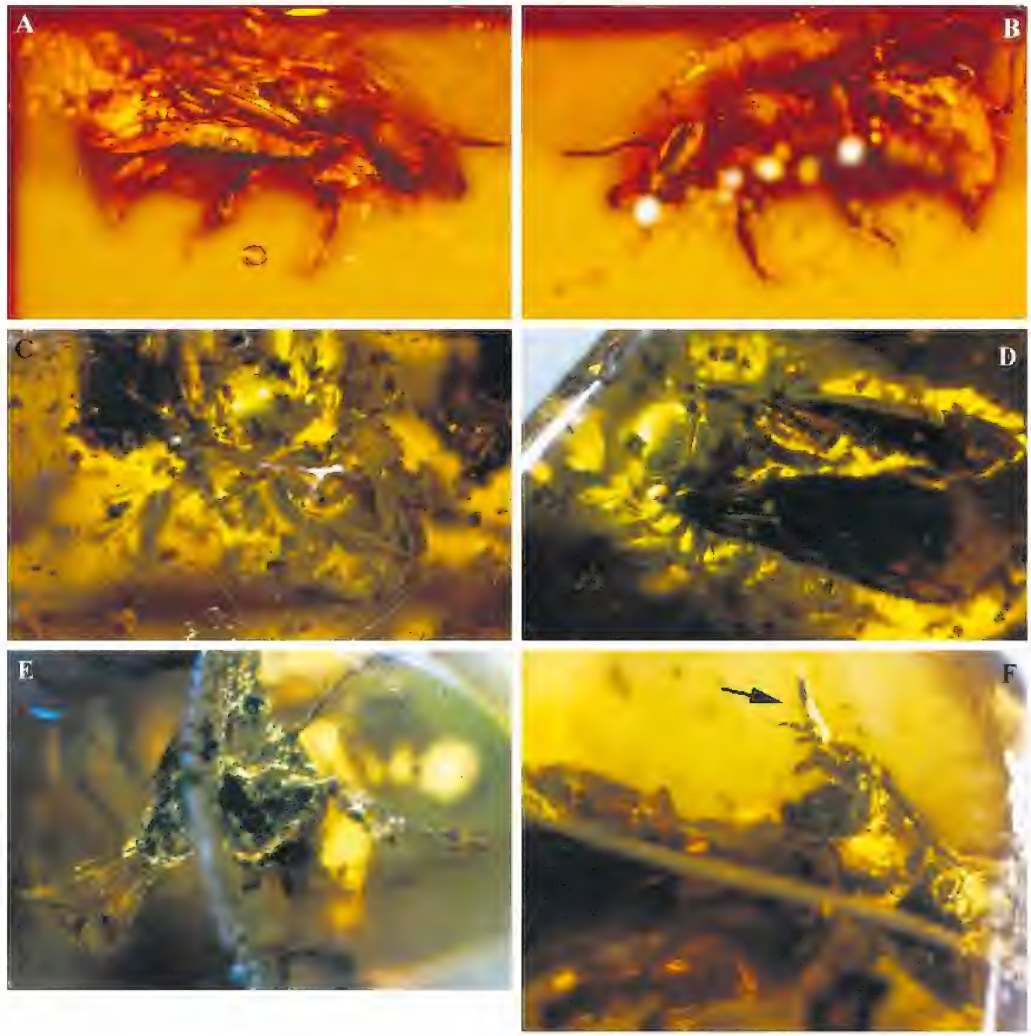


Plate 1. Families Halictidae, Paleomelittidae, and Melittidae. **a.** *Electrolictus antiquus* Engel, holotype female (MB.I.1952 ZMHB), right lateral view. **b.** *E. antiquus,* holotype female, left lateral view. **c.** *Paleomelitta nigripennis* Engel, holotype female (B-JH 101 AMNH), frontodorsal oblique view. **d.** *P. nigripennis,* holotype female, dorsal view. **e.** *Eomacropis glaesaria* Engel, holotype female (SAMH), frontal view of head. **f.** *E. glaesaria,* holotype female, left lateral view with arrow indicating staphyliniform larva on dorsum.

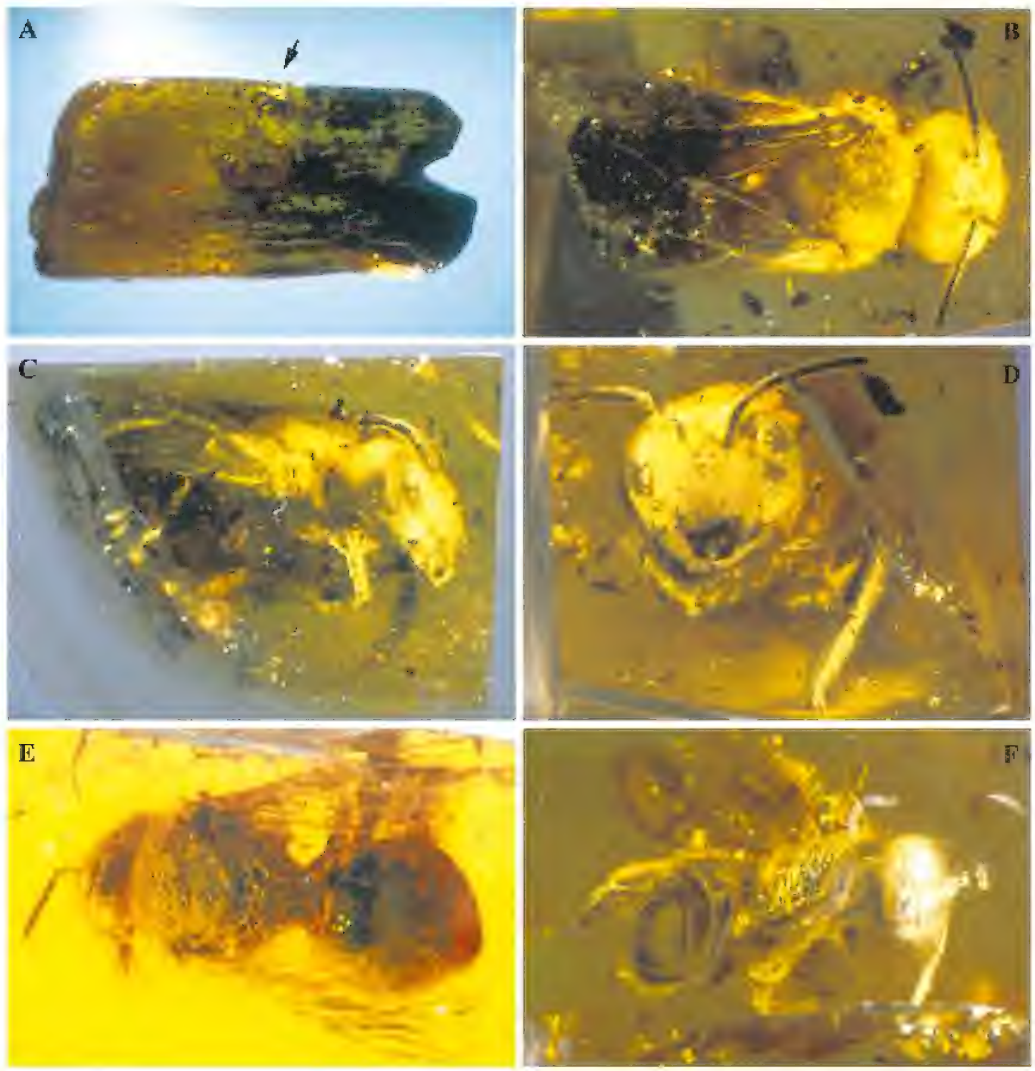


Plate 2. Families Paleomelittidae and Megachilidae (Lithurginae and Glyptapina). **a.** Amber block with inclusions of *Paleomelitta nigripennis* Engel (B-JH 101 AMNH), position of holotype indicated by arrow (visible dimensions of block: width 5.5 cm, length 13.5 cm). **b.** *Protolithurgus ditomeus* Engel, holotype female (B-W 157 AMNH), dorsal view. **c.** *P. ditomeus,* holotype female, right lateral view. **d.** *P. ditomeus,* holotype female, frontal view of head. **e.** *Glyptapis mirabilis* Cockerell, holotype female (K72 IMGP), dorsal view. **f.** *G. disareolata* Engel, holotype female (B-JH 104 AMNH), ventral view.

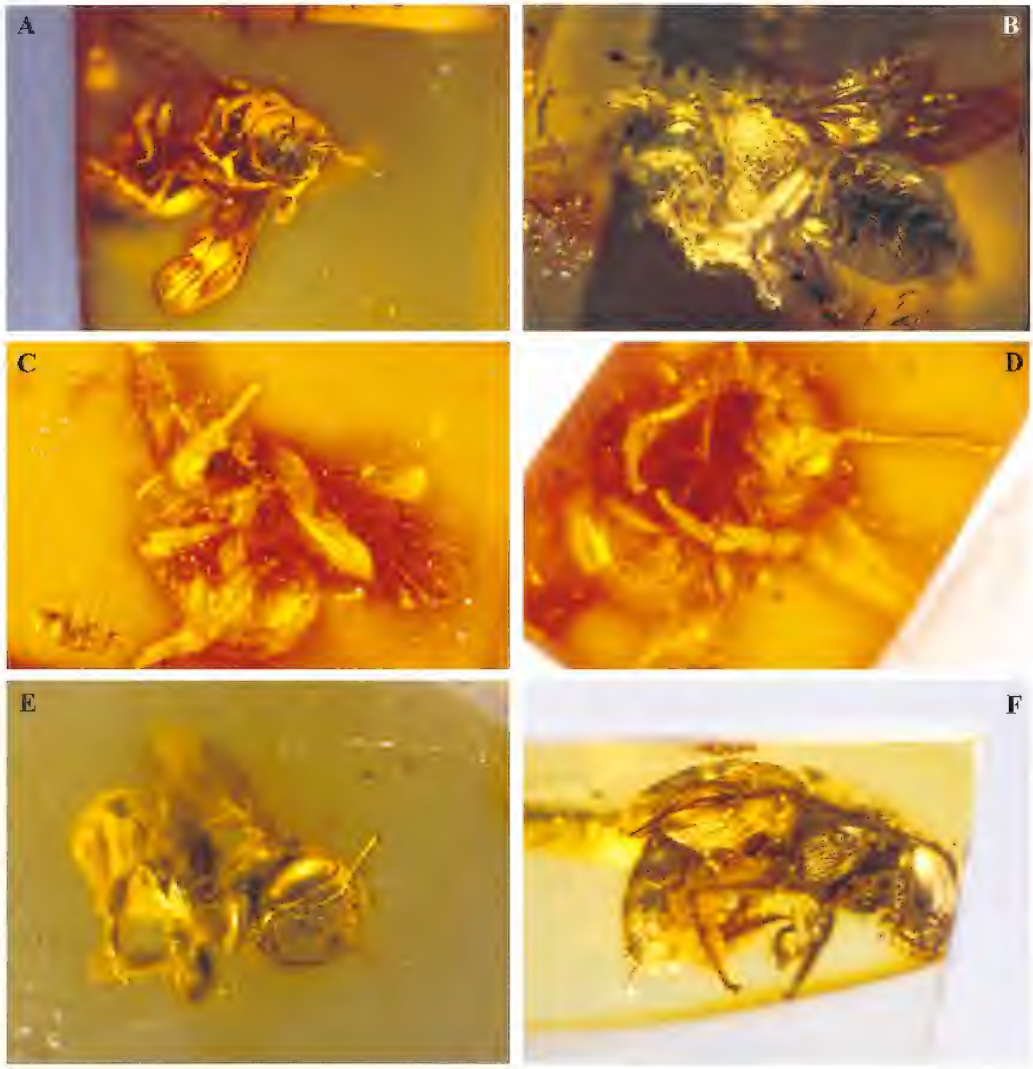


Plate 3. Family Megachilidae: Glyptapina and Ctenoplectrellina. **a.** *Glyptapis fuscula* Cockerell, female (ZMUC), frontal view of face. **b.** *G. densopunctata* Engel, holotype female (B-W 161 AMNH), left ventrolateral oblique view. **c.** *Ctenoplectrella viridiceps* Cockerell, male (NB.I.1949 ZMHB), left lateral view. **d.** *C. viridiceps,* male, ventral view. **e.** *C. viridiceps,* neotype female (B-JH 95 AMNH), right frontolateral oblique view. **f.** *C. grimaldii* Engel, holotype female (B-JH 88 AMNH), right lateral view.

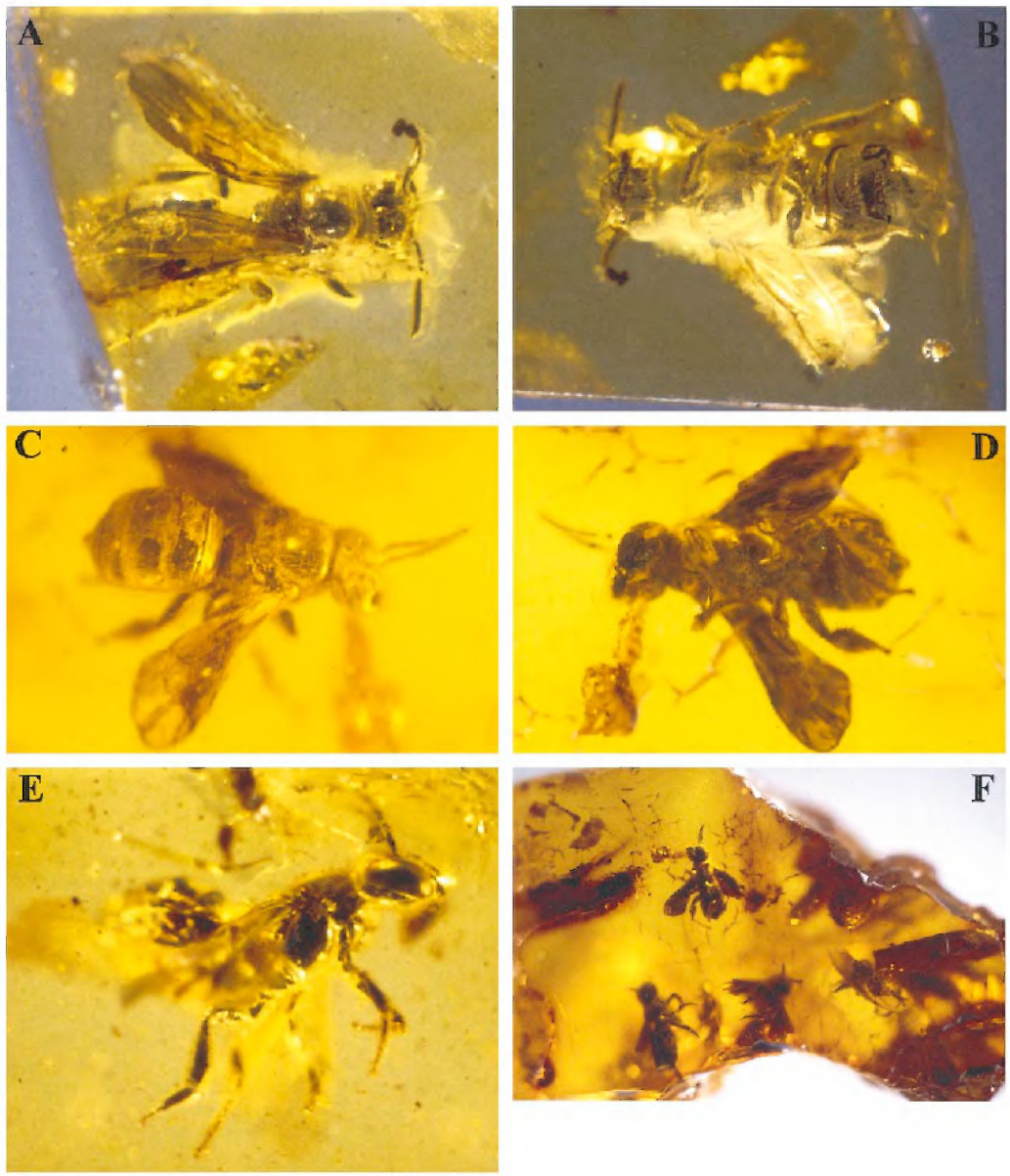


Plate 4. Family Apidae: Xylocopinae. **a.** *Boreallodape baltica* Engel, holotype female (B-JH 152 AMNH), dorsal view. **b.** *B. baltica,* holotype female, ventral view. **c.** *B. striebichi* Engel, holotype female (B-BS 153 AMNH), dorsal view. **d.** *B. striebichi,* holotype female, ventral view. **e.** *B. mollyae* Engel, holotype female (B-JH 81 AMNH), right lateral view. **f.** Amber block with inclusions of *B. striebichi,* holotype female is the uppermost specimen to the left of a flower fragment and highlighted by light source (visible dimensions of block: maximal width 2.1 cm, length 3.7 cm).

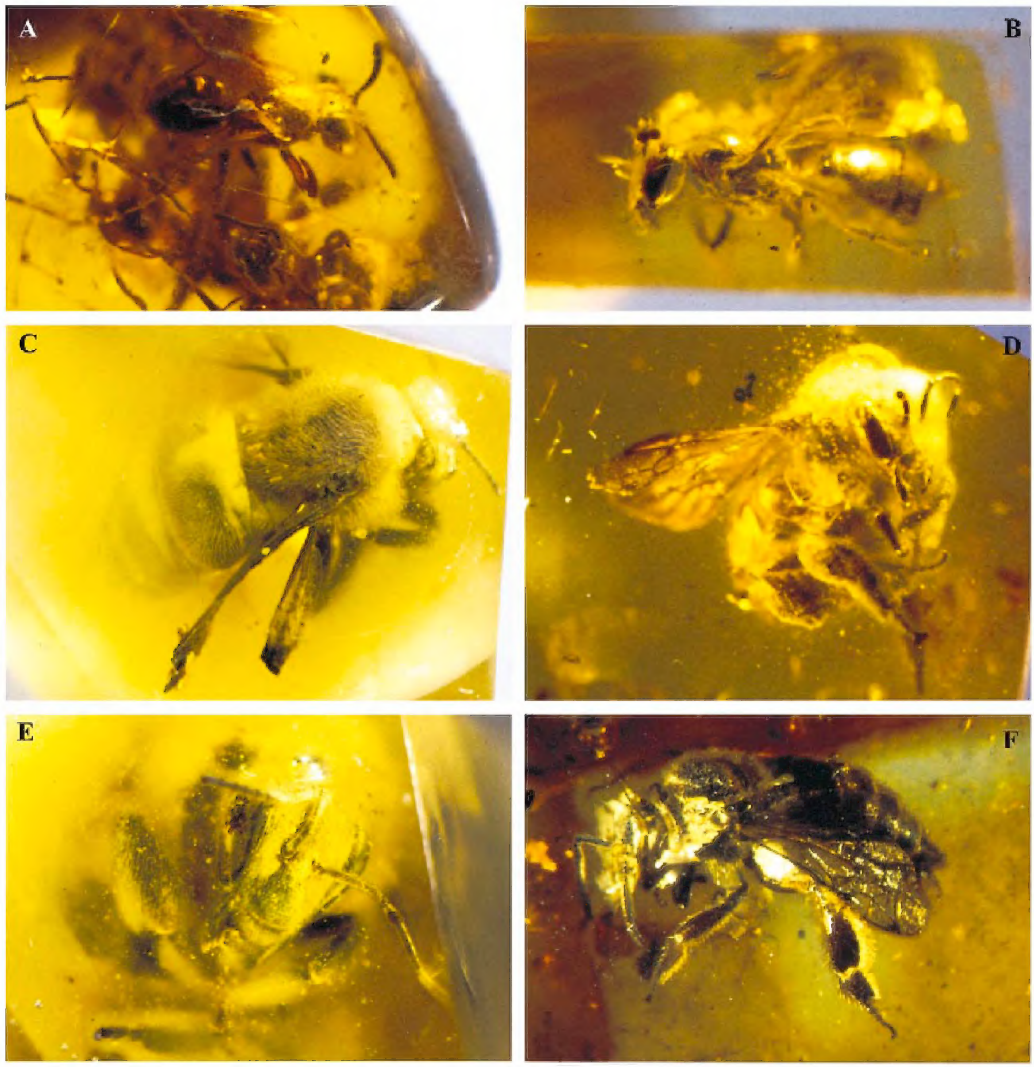


Plate 5. Family Apidae: Xylocopinae, Electrobombini, and Electrapini. **a.** *Boreallodape mollyae* Engel, paratype female (19948 ZMPA), dorsal view. **b.** *B. baltica* Engel, holotype female (B-JH 152 AMNH), left lateral view. **c.** *Electrobombus samlandensis* Engel, holotype female (B-JH 94 AMNH), dorsal view. **d.** *Protobombus hirsutus* (Cockerell), neotype female (B-JH 92 AMNH), frontolateral oblique view. **e.** *E. samlandensis,* holotype female, frontal view of head. **f.** *Thaumastobombus andreniformis* Engel, holotype female (B-JH 164 AMNH), left lateral view.

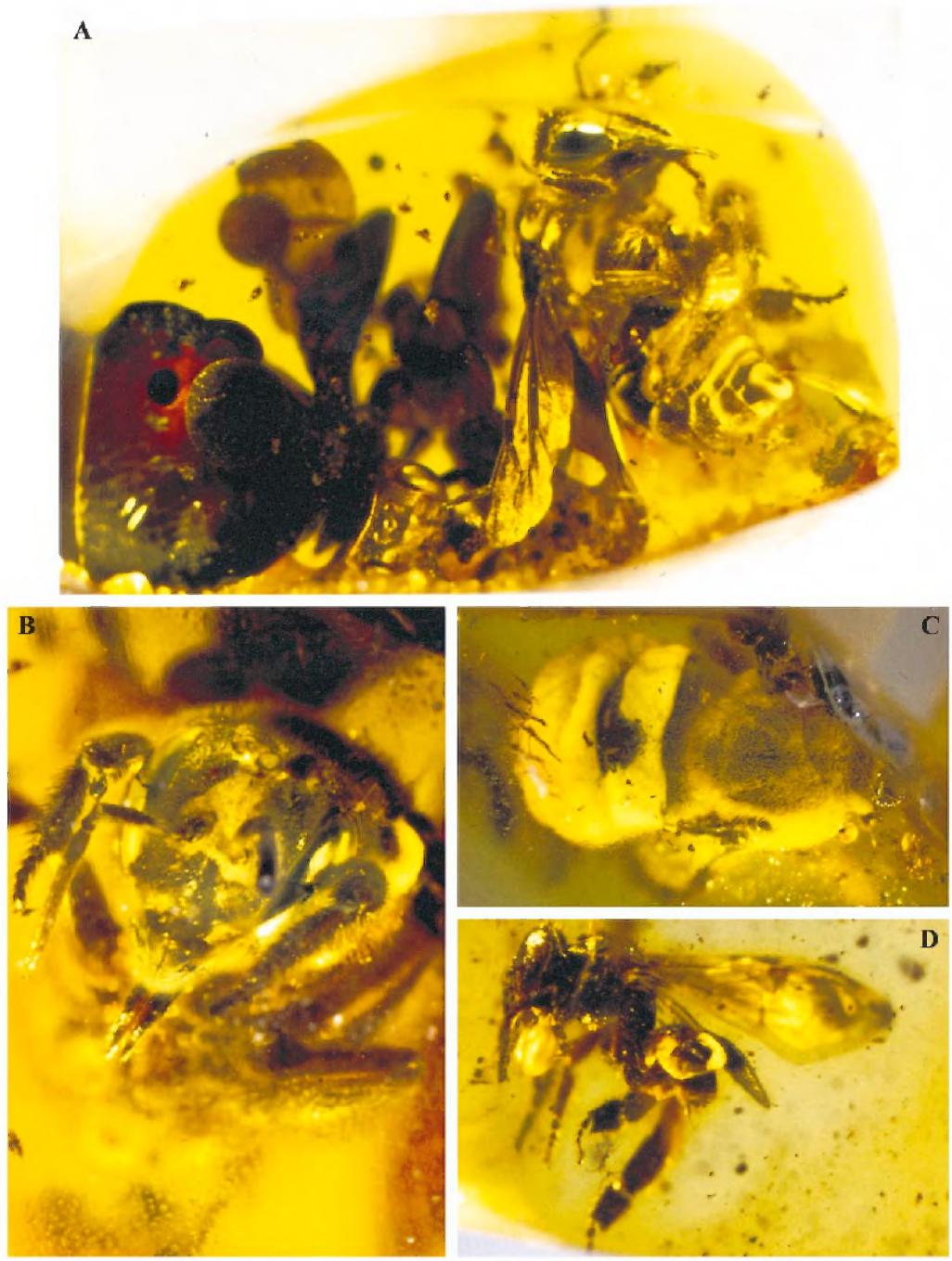


Plate 6. Family Apidae: Electrapini and Melikertini. **a.** *Protobombus indecisus* Cockerell, neotype female (B-JH 98 AMNH), right lateral view; neotype is individual in left of photograph, the head of a second specimen is visible along the lower margin near the hind wing apex of the neotype. **b.** *P. indecisus,* neotype female, frontal view of head. **c.** *Electrapis meliponoides* (Buttel-Reepen), neotype female (B-JH 97 AMNH), dorsal view. **d.** *Melissites trigona* Engel, holotype female (B-JH 102 AMNH), left lateral view.

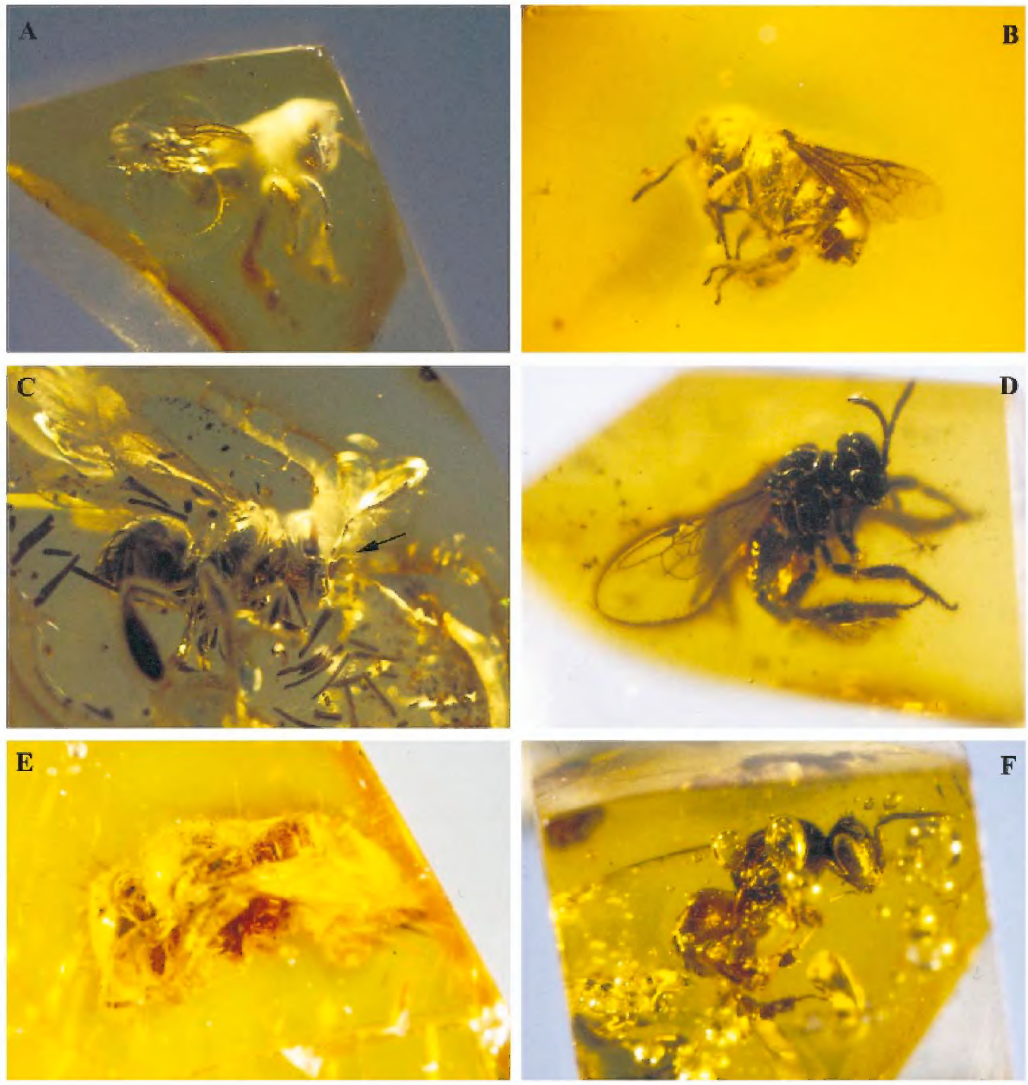


Plate 7. Family Apidae: Melikertini and Meliponini. **a.** *Melikertes clypeatus* Engel, holotype female (B-JH 77 AMNH), right lateral view. **b.** *Succinapis proboscidea* Engel, paratype female (B-JH 99 AMNH), left lateral view. **c.** *S. micheneri* Engel, holotype female (B-JH 103 AMNH), right lateral view (arrow indicates clypeal protusion). **d.** *S. goeleti* Engel, holotype female (B-JH 90 AMNH), right lateral view. **e.** *Kelneriapis eocenica* (Kelner-Pillault), holotype female (NB.I.1946 ZMHB), left lateral view. **f.** *Liotrigonopsis rozeni* Engel, holotype female (B-JH 79 AMNH), right lateral view.